Spatial scale and nest distribution of little penguins (*Eudyptula minor*)

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Statements by the author

Declaration of Originality

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The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University. This project was undertaken with University of Tasmania Animal Ethics Committee permits A0010360 and A0012146. Permits from Parks and Wildlife Service were FA 1003, FA 11011 and FA 12006.

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Abstract

The breeding habitats of all seabirds are not uniformly distributed spatially and temporally, but typically exist as discrete patches. Most species of seabirds breed in colonies that vary in size, and are generally located close to foraging areas. These colonies typically form patterns in the landscape and maintain some inter-connectivity that can be at the genetic and / or demographic levels.

Interactions between abiotic and biotic factors determine the extent and distribution of a population in a geographical area. Temporal factors such as the seasonal variation in the availability of food and breeding season phenologies also determine spatial and temporal species distributions. This study investigates the abiotic and biotic interactions that can operate in a hierarchical series of habitat spatial scales extending from the *Meso* (100s – 1000s km), *Topo* (100s m), *Micro* (10s m) to *Nano* (1+ m) scales.

The spatial distribution of colonies and nests of a burrowing seabird, the little penguin (*Eudyptula minor*) found along the North West Coast of Tasmania are investigated. These colonies are recognised to be a component of the little penguin metapopulation that has been identified for south-east Australia. The metapopulation embraces the concepts of source-sink colonies and that of the role of habitat quality. The spatial distribution of little penguin colonies was investigated at different spatial scales, and the relationships between habitat, nest-site quality, microclimate and chick productivity are examined as the spatial scale decreased from landscape to individual nest-sites.

In this thesis, I present data and analyses that examine:

1) *Spatial distributions of little penguin and burrows*. Geographical Information Systems (GIS) were used to analyse the spatial patterns of colonies along the North-West Coast of Tasmania. Data collected using differential GPS were analysed in order to describe the distribution of nest-sites within and among colonies. The spatial analyses showed that colonies were not distributed randomly and that nest-sites were clustered within colonies.

2) *Environmental factors influencing nest distribution*. A habitat model was used to statistically explain the presence or absence of burrows. The model was developed using the following terrain variables: elevation, slope, aspect (extracted from a high resolution 1 m × 1 m DEM); and calculated solar radiation and wetness index. The distance to the coast was also calculated for each presence and absence point included in the model.

3) *Microclimate of burrows*. Temperature and relative humidity were measured in different burrow types (grass, sand, vines and artificial) over the main period of the breeding season to investigate the extent of microclimate variation within and among burrow types. The relationship between the burrow and external temperature was also examined among the burrow types. The frequency with which the burrow temperatures exceeded 27ºC, the Upper Critical Temperature (UCT) at which penguin chicks may experience difficulty in thermoregulation, was also determined.

4) *Influence of burrow type on breeding success*. The presence or absence of chicks as well as the number of chicks produced per burrow type was analysed during three breeding seasons using GLMM to investigate whether there was a difference in the productivity per burrow type.

The use of spatial habitat scales in the analyses of a burrowing seabird and the examination of abiotic and biotic factors (and their interactions) has provided new insights into how little penguins interact with their environment at a range of spatial scales. The study has also developed a novel approach to investigating the relationships between the distribution of seabirds and their habitat.

New findings have emerged in three areas of seabird ecology:

(i) The spatial analyses of seabird colonies undertaken by GIS showed a dispersed pattern of distribution at both the *meso*- and *coarse* scales, yet within the colonies the nest-sites were clustered.

(ii) A habitat model based on a range of terrain variables provided a statistically valid model to explain the presence, but not the absence, of burrows within colonies. This may be the result of the presence of suitable habitat that is underutilised by the penguins or that space is not a limiting factor, or other factors such as vegetation cover that may also be necessary to model habitat utilisation more accurately.

(iii) Microclimate variations were not uniform among the burrow types, and some burrow types were more prone to exceed the UCT of 27ºC in a way that could be potentially harmful to adult penguins and their chicks.

(iv) Chick production during three years of this study was higher in artificial burrows compared to the natural burrows. The implications of the findings of this study are discussed in terms of conservation and management in peri-urban environments of little penguin colonies.

Acknowledgments

Undertaking a PhD feels like a very long journey where you never quite know where you are going at times and if you will ever arrive at a destination. There are always unforseen twists and turns, and surprises along the way. More often than not, it feels like a roller coaster. One thing is certain, it is not a journey one undertakes alone.

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Contents

CHAPTER 1

Introduction

1 Introduction

1.1 Spatial scale in landscape ecology

The central focus of landscape ecology is to identify local and factors that strongly influence the spatial between ecological patterns and processes (Turner 1989; Levin 1992). The term "Landscape ecology" was introduced by the German biogeographer Carl Troll in the late 1930s and now essentially combines the spatial approach of the geographer with the functional approach of the ecologist (Turner *et al.* 2001).

Spacing or spatial arrangement is a scaled property of living organisms, from individuals to populations, communities and metapopulations (Farina 2008). Spacing can be described as the ecological reaction of organisms to a non-uniform distribution of resources (habitat suitability) and to intra – and interspecific competition in space and time. Consequently, the distribution patterns of individual species are seldom in a uniform and continuous in space and time, so the identification of influencing factors is a primary concern in ecological studies (Caughley 1977; Morrison & Hall 2002). The distributions of all species *in toto* are experienced at a landscape level, and so at a much greater spatial extent than that normally studied in ecology (Turner 1989). The emphasis of landscape ecology is to identify scales that best characterise relationships between spatial heterogeneity and biophysical processes of interest for ecological interpretation (Turner 1989). Clearly, no single scale is appropriate for all ecological questions. Some questions focus on individual organisms, and how they respond physiologically to environmental conditions and change. Other questions may focus on how numbers of species may change as a result, for example, of competition for limited resources. Other valid questions may relate to the scale of the entire population, of the metapopulations, or the interactions among these populations (Turner 1989).

One of the emerging ways to model and interpret the distribution of a species is to examine both the environmental (resources such as light, heat, water and nutrients) and behavioural (requirements such as to seek food, shelter, reproduce, minimise competition and avoid predation) factors that are known to influence, or may be correlated with, the observed spatial distribution of individuals. This approach provides a logical framework to interpret the distribution of species using 'nested hierarchies' (Mackey & Lindenmayer 2001). The environmental hierarchy considers a nested hierarchy of abiotic and biotic processes that may determine the distribution of available resources; the behavioural hierarchy evaluates the distribution of species 'units' in the context of varying scales of habitat (Mackey & Lindenmayer 2001). The unit may be an individual, a pair at a nest-site, a group of animals within a colony, a population in a region, a metapopulation over a much larger space, or the total geographic distribution of a species. At each unit level, diurnal, seasonal and annual

changes in environmental factors may influence the behaviour of species - such as the timing of breeding season onset.

Examination of a combination of environmental and behavioural factors at different spatial and temporal scales may provide a more realistic understanding of how a species utilises its habitat. For example, predictions of the broad distributional limits of a species may not provide sufficient information to understand and predict the requirements for species persistence at a site or local level. This may be the case particularly for species that forage widely, but return to restricted localities to breed.

The interactions of abiotic and biotic factors determine the distribution of organisms in a landscape (Levin 1992). Temporal factors such as seasonal differences in the availability of food, timing of breeding seasons and even variation in body condition are important. These spatial and temporal factors then generate patterns at scales that are rarely uniform or continuous (Morrison & Hall 2002). At smaller scales some nest-sites are indeed uniform in distribution especially in sea birds that nest on the surface of the land in order to minimise antagonistic behaviours. Understanding how the distribution of populations of animals is spatially scaled in the landscape is an important aspect of the ecology of any species (Goodwin & Fahrig 1998; Mackey & Lindenmayer 2001; Austin 2007; Krebs *et al.* 2013).

Populations can be organised into different hierarchical levels from the individual to the global population that respectively form the lower and upper limits of the potential scales of a species distribution (Figure 1-1). The term "ecological neighbourhood" defines the range over which an individual moves during its usual activities (Addicott *et al.* 1987). The range over which an animal moves defines its neighbourhood; for a highly mobile animal the range may be very large, and for a sessile animal quite restricted. The ecological neighbourhood can also vary depending on the life cycle stage of an animal. For example, the ecological neighbourhood of a nesting seabird can be quite small and focussed on the terrestrial habitat and proximity to foraging grounds; during the non-breeding season, foraging may be more widespread and the ecological neighbourhood may be much larger. Ecological neighbourhoods vary with space and time, and are affected by different processes; this is a general concept that can apply to different scales of habitat (Addicott *et al.* 1987).

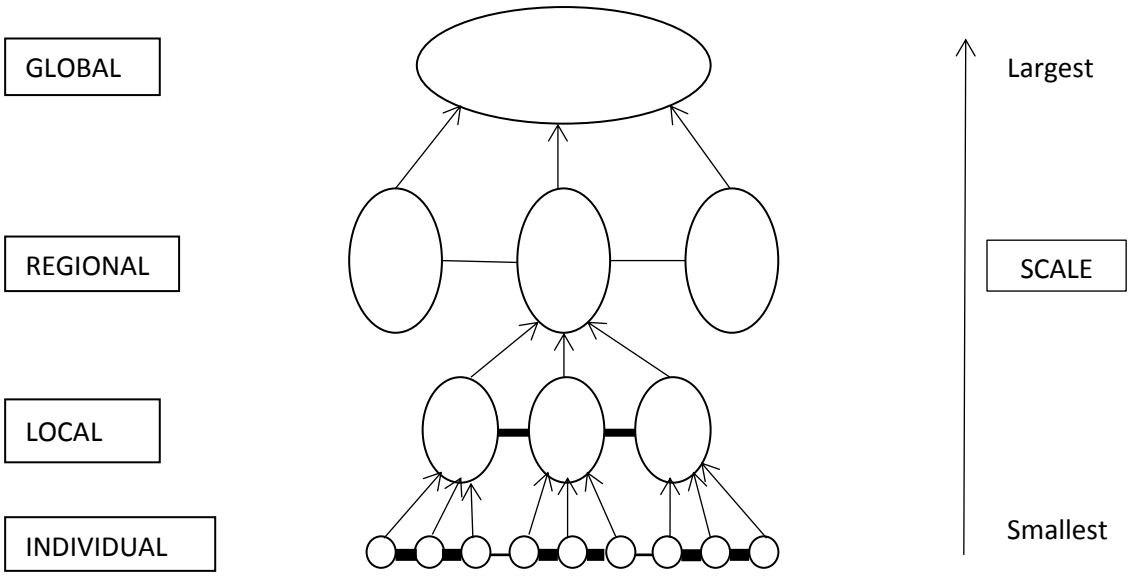


Figure 1-1 *Diagrammatic representation of the organisation of populations of a species at different spatial scales. Spatial habitat scale is smallest at the individual level and largest on the global level. Degree of probability of interaction among the groups is represented by the thickness of the lines (from Goodwin et al 1998). The degree of interaction between each entity at each level decreases as the degree of spatial aggregation increases, as indicated by the thickness of the arrows. The probability of individuals interacting with each other is much greater within a small scale than individuals interacting with each other in different regions.*

Scale has two important characteristics: *grain* which refers to the smallest unit, the minimum spatial resolution of data in a raster (e.g. 1 m^2), or measured in the field (e.g. a quadrat), and *extent* which defines the size of the spatial area over which a study is undertaken and for which data are available (Turner *et al.* 1989). To avoid confusion, "scale" typically refers to the resolution or *grain* at which patterns are measured, perceived or represented (Morrison & Hall 2002).

Various frameworks are used to study animal and plant distributions from a multi-scale perspective (Stommel 1963). Scale was used to develop relationships between physical ocean processes and the occurrence of plankton. This included various temporal and spatial scales. Zooplankton biomass has also been modelled at the same scales (Haury & Pieper 1988). Ecological scale has been the subject of studies of many plants and animals (see references in Weins 1989 and Mackey et al 2001), including birds at sea (Haury & Pieper 1988). These authors defined the following scales; *mega* (3000 km); *macro* (1000 - 3000 km); *meso* (100 - 1000 km); *coarse* (1 - 100 km) and *fine* (1 - 100 m). Using these scales, oceanographic factors have been related to the spatial dynamics of birds at sea (Hunt Jr & Schneider 1987).

A hierarchical scale of habitat developed for leadbeaters possum (*Gymnobelideus leadbeateri)* used five levels which were based on classifying animal distribution in biological units from large to small: *global, meso, topo, micro* and *nano* scales (Mackey & Lindenmayer 2001). The *global* and *meso* scale included all populations of the leadbeaters possum, whilst the *topo* scale included behavioural aspects related to interactions among populations. Dispersal mechanisms, dispersal capability and metapopulation dynamics were included at this *topo* scale. The *micro* scale included aspects of the colony structure such as presence of hollow-bearing trees and *Acacia spp* understorey trees that supported the presence of the leadbeaters possum. The *nano* scale considered thermoregulation and energy conservation properties of the nests (Mackey & Lindenmayer 2001). Each level has an associated spatial scale and properties that are not the summation of the disaggregated parts (Mackey & Lindenmayer 2001).

This study adopts a similar scale for seabirds: *global, meso, topo, micro* and *nano* (Table 1-1). These five levels represent natural breaks in the spatial scales of the distribution and availability of resources, and in the role of abiotic and biotic factors in the terrestrial environment.

Spatial ecology focuses on understanding and explaining the processes that affect the spatial distribution of organisms in their environment (Gremillet & Boulinier 2009). Spatial patterns can be observed at more than one scale and a holistic approach for understanding how global factors can influence the distribution of a species at the local level is growing in importance (Chave 2013). An example of this is demonstrated in Table 1-1, which shows how abiotic and biotic factors may influence responses in seabird colonies.

Table 1-1 *Proposed scalar hierarchy for breeding seabirds (adapted from Stommel (1963) and Mackey and Lindenmayer (2001). The highest resolution is at the nano scale.*

Spatial scale	Abiotic and biotic environmental processes acting on spatial scale	Behavioural responses of seabirds at spatial and temporal scale
Global – geographic distribution of whole species **(100s – 1000s km)**	Latitudinal and seasonal variation in solar radiation. Oceanographic and atmospheric circulations.	Establishment and persistence of nesting colonies and foraging areas of a species.
Meso – distribution of colonies **(100s – 1000s km)**	Regional oceanographic and atmospheric conditions that influence foraging zones. Seasonal variations in abundance and distribution of prey. Variations in regional distribution of vegetation used for nesting.	Fluctuations in population numbers due to metapopulation dynamics of colonies in a region. Establishment and disappearance of colonies.
Topo - nest-site density and pattern within a colony **(100s m)**	Local topographic variations that influence terrain variables (such as elevation, aspect, slope).	Influence of spatial distribution of nest-sites on social interactions among nesting seabirds. Allee effect.
Micro – characteristics of individual nest-sites **(10s m)**	Influence of micro-climate on individual nests. Influence of density-dependent factors such as predators and ecto-parasites.	Selection of individual nest-sites.
Nano - individual seabirds **(1s m)**	Seasonal variation in temperature, precipitation affecting thermoregulation of chicks, particularly during the breeding season. Climate variations may affect the food supply.	Successful characteristics for breeding (life span, age, experience) of individuals in selection of mates, predator avoidance.

1.2 Metapopulations

A metapopulation consists of several spatially separated populations of the same species in a patch network within areas of suitable habitat (Hanski 1998; Schippers *et al.* 2009). The concept of a metapopulation was first described in a study on parasites in 1935 (Nicholson & Bailey 1935). They stated:

"A probable ultimate effect of increasing oscillation is the breaking up of the species – population into numerous small, widely separated groups which wax and wane and then disappear, to be replaced by new groups in previously unoccupied situations"

Nicholson and Bailey (1935, p 590).

In classical metapopulation theory, interaction occurs at some level among the populations within the metapopulation. However, each population exists in relative independence and eventually may be extirpated as a consequence of demographic factors. The smaller the population, the more prone it is to extinction because of predation, disturbance to the habitat, and the Allee effect. This effect is defined as "a positive relationship between any component of individual fitness and either numbers or density of conspecifics" (Stephens *et al.* 1999). Stochastic events such as disease outbreaks or storms can also impact smaller populations. The component aspect would take the form of a metric such as the probability of death or reproduction being higher than in a larger population.

Although individual populations may have finite life-spans, the metapopulation *in toto* is often stable because immigrants from one population can re-colonise habitat which has been left open by the extirpation of another population. Metapopulation theory (Levins 1969; Hanski 1998) and the concept of source – sink populations which both recognise the heterogeneity of habitat (Pulliam 1988; Bansaye & Lambert 2013; Fernandez-Chacon *et al.* 2013), reinforce the importance of connectivity between and among apparently isolated populations. Although it is unlikely that a single population may be able to guarantee the long-term survival of a given species, the interconnections, including genetic relatedness, between many discrete populations may be able to facilitate the long-term persistence of a species in a defined area.

Populations of many species tend to consist of several patches that are connected by dispersal between the patches to some extent (Figure 1-1). Since habitat quality is likely to be heterogeneous and to vary among patches, it is important to consider how a low quality patch might affect a population. In terms of source – sink population dynamics, organisms theoretically can occupy two patches of habitat. One patch, the source, is a high quality habitat that generally allows the population to increase; the second patch, the sink, is generally low quality habitat that, on its own, may not be able to support a population. However, if the excess of individuals produced in the source frequently moves to the sink, the sink population can persist indefinitely and can be quite large (Van Horne 1983; Pulliam 1988).

Criteria that characterise the difference between low and high quality habitat are required in order to understand how organisms select between source and sink habitats (Fernandez *et al.* 2007). The population density of the organism is not necessarily an indicator of good habitat, as in good years the density in the lower quality habitat may be greater than in the higher quality habitat (Van Horne 1983). Seasonal variation, temporal unpredictability and patchiness are factors have been identified to increase the probability that population density will not be positively correlated with habitat quality. For example, the population density of field sparrows (*Spizella pusilla*) may be relatively high in an area due to a high rate of immigration, but breeding success may be relatively low; consequently the high number of birds may create the false impression of good habitat quality (Fretwell 1969).

Ecological trap theory (Kristan 2003) suggests that under some circumstances a sink habitat is preferred over a source habitat, leading to a steady decline of the population. This can occur when there has been a sudden alteration to a habitat where previously reliable cues for species behaviour are no longer associated with adaptive outcomes (Schlaepfer *et al.* 2002). The source-sink model implies that some habitat patches may be more important than others to the long-term survival of a population. Identifying sources and sinks, and understanding source-sink dynamics, are relevant to conservation and management decisions in these contexts. An understanding of the characteristics of the habitat would assist in understanding the source-sink dynamics that may exist in different habitats. Of course, estimates of demographic parameters including recruitment, dispersal and survival rates in different habitats would also be required to confirm the source-sink concept of habitats.

1.3 Seabird Colonies

Seabirds have adapted to life in the marine environment and typically breed in dense colonies (Marchant *et al.* 1990; Schreiber & Burger 2001). The adaptive significance of colonial breeding has been well covered (Wittenberger & Hunt Jr 1985; Schreiber & Burger 2001). Most of the colonies are usually on offshore islands or coastal areas (Cody 1973; Furness & Monaghan 1987). Their distribution is influenced by the dispersal and availability of prey in marine ecosystems (Gremillet & Boulinier 2009). All seabirds are dependent on land to breed and the availability of suitable breeding habitat in terrestrial systems is thought to play a significant role in regulating seabird population and growth (Brooke 2004; Dann & Norman 2006).

Seabirds comprise the Sphenisciformes (penguins), Procellariiformes (albatrosses, petrels, storm-petrels, fulmars and shearwaters), Pelecaniformes (pelicans, frigatebirds, gannets, boobies, cormorants, anhingas) and Charadriiformes (shorebirds, skuas, jaegers, gulls, terns, skimmers, guillemots, puffins and auks) (Schreiber & Burger 2001). Seabirds may switch

between marine and terrestrial habitats on a frequent basis, which can be as frequently as daily during the breeding season.

Seabirds operate at a wide range of spatial scales, from their foraging activities over 1000s of kilometres of ocean to the selection of a nesting site at a scale of a few metres. They typically breed in aggregations (hereafter referred to as 'colonies', which can be synonymous with the term 'populations' in metapopulation theory) that exchange individuals at varying rates depending on the species. With reference to seabirds, Buckley et al. (1992) define a metapopulation as:

"*an interacting cluster of intermittently occupied, discrete sites which exchange breeders"*.

This definition specifically emphasises that sites supporting seabird colonies can be vacant or unoccupied at times (Buckley & Downer 1992). It has been suggested that competition for resources within and among neighbouring colonies modifies their distribution and size (Furness & Birkhead 1984). Colonies in close proximity to each other may be part of a metapopulation and what appear to be discrete and possibly independent colonies may in fact be linked by dispersal (Newton 1998).

The highly philopatric nature of many seabirds means that adaptation to changing environmental conditions such as shifting prey distributions linked to climate change or fishing may be problematical. The long delay in reaching sexual maturity of many seabird species provides enough time for the birds to build up a memory bank of the dynamics of prey patches and possibly ways of optimising foraging (Gremillet & Boulinier 2009; Weimerskirch *et al.* 2010). After sexual maturity, however, the memory bank may be detrimental if the birds are then unable to adapt to further changes in environmental conditions (Chambers *et al.* 2005; Chambers *et al.* 2011).

1.4 The study species

Little penguins *(Eudyptula minor*) are irregularly distributed in colonies of varying sizes in southern Australia and New Zealand (Marchant *et al.* 1990). They are found on Penguin Island in Western Australia, around the coast of the Great Australian Bight in numerous colonies , on offshore islands in Bass Strait, and along the east coast of Victoria and southern New South Wales and adjacent offshore islands in a few locations (Figure 1-2). Some little penguin colonies are located in urban areas such as at St Kilda in Melbourne and Manly in Sydney. They are also found along coasts and on offshore islands in Tasmania (Figure 1- 2). Their life cycle and various aspects of their ecology, demographics, breeding biology, diet, foraging, responses to environment, nesting behaviour and physiology have been studied extensively in Victoria (Cullen & Dann 1988; Cullen *et al.* 1992; Dann *et al.* 1992b; Harrigan 1992; Chiaradia & Kerry 1999; Collins *et al.* 1999; Chiaradia *et al.* 2003; Dann *et al.* 2003; Dann & Norman 2006; Dann

& Chambers 2013), Western Australia (Klomp *et al.* 1988; Klomp & Wooller 1988; Klomp *et al.* 1991; Wienecke 1995; Wienecke *et al.* 2000; Cannell *et al.* 2012), New South Wales, (Rogers *et al.* 1995; Priddel *et al.* 2008), South Australia (Bool *et al.* 2007) Tasmania (Gales *et al.* 1988; Stevenson & Woehler 2007) and New Zealand (Bull 2000; Johannesen *et al.* 2002; Agnew *et al.* 2014).

Phylogeographic studies on the little penguin suggest that a single sub - species exists in Australia with several discrete metapopulations indicated by the blue dotted lines in Figure 1-2 (Peucker *et al.* 2009; Burridge *et al.* 2015). The overall size of the whole population in Australia has been estimated at 454,000 birds, with 60% of the population located in the Bass Strait area (Dann *et al.* 1996).

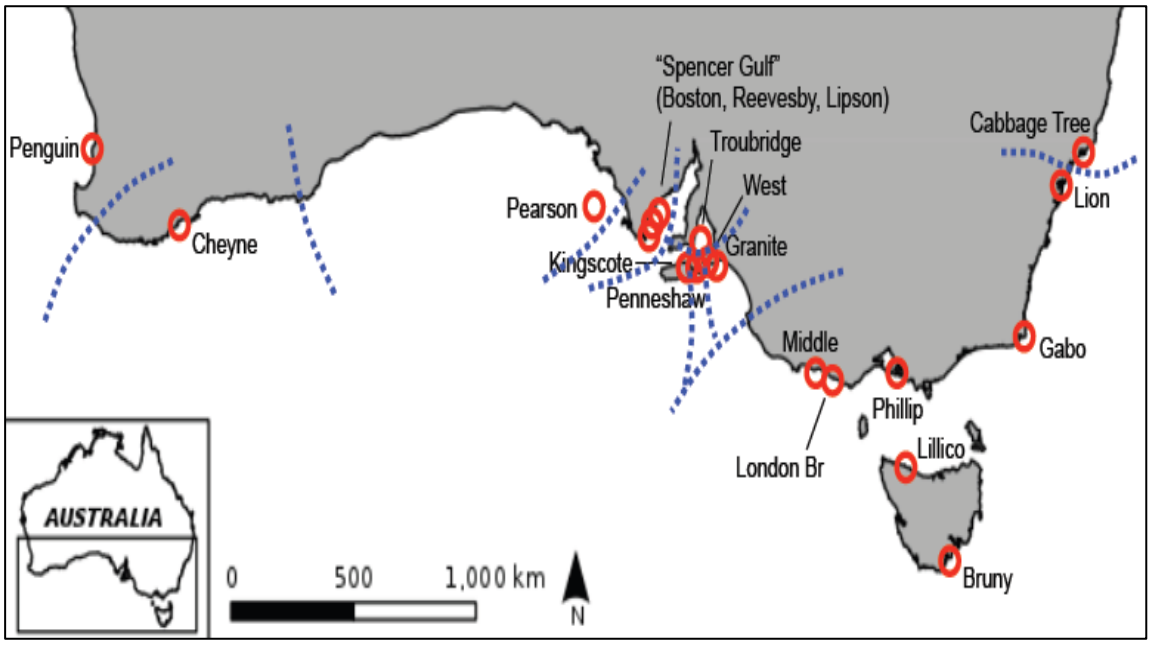


Figure 1-2 *Metapopulation boundaries of little penguin distribution in Australia. Tasmania's population is shown as part of the SE group (Figure courtesy of C. Burridge 2013). The red circles represent study sites for the phylo-geographic study of little penguins (Peucker et al. 2009) whilst several discrete metapopulations are indicated by the blue dotted lines (C.Burridge pers comm).*

1.5 Study area

The distribution of little penguins in Tasmania is mostly concentrated on the offshore islands, but colonies are also found around the coastal areas of mainland Tasmania. Many of these exist along the northern coast. This study focussed on colonies along the North West Coast (the name adopted for this population in this thesis). In 2000, up to 5700 little penguins were estimated to be present within 17 colonies of varying sizes that are dispersed along a 50 km stretch of the North West Coast (Marker, unpublished data). They form the basis of this study either at the colony or nest-site level. The habitat has been heavily modified anthropogenically with most colonies existing in peri-urban or urban areas. These colonies are

also restricted to coastal areas that have fences preventing access inland. Seventeen colonies over such a small distance is an unusually high number for little penguins as typically individual colonies are more isolated. It is this close distribution of the colonies that makes this an interesting case study.

1.6 Use of Spatial Technology

In order to produce reliable maps of species' distribution and habitat suitability, the type and quality of data collected are important. For example, the collection of historical as well as new field data on species distribution, as well as information on associated environmental processes, has been shown to be important for habitat analyses using GIS and modelling. In developing a model, the data collected and processed need to be as accurate and precise as possible, with minimal errors and bias. This allows a better evaluation of the hierarchy levels as each level is dependent on the level below (Van Horne 1983). Output accuracy will only be as good as the input data and tools used in the process.

1.6.1 Global Positioning System (GPS)

In this study, a differential GPS (DGPS) was used, as accuracy was important for habitat model development. A hand held GPS may identify a point to within 5- 10 m accuracy whereas a DGPS has an accuracy of 0.2 m and is more reliable. Information on how DGPS functions and how it improves accuracy is provided in appendix 1.

1.6.2 Digital elevation model (DEM)

Digital elevation models (DEM) are often used to study species habitat as they provide terrain and topographic variables that are related to environmental gradients. The primary attributes provided by DEMs are elevation, slope, and aspect. Secondary attributes such as solar radiation and topographic wetness index are calculated from the primary attributes. Systematic and non-systematic errors contained in DEMs, along with the resolution of the elevation grid, can affect the derivation of the primary and secondary terrain attributes (Franklin 2009).

1.7 Management

As little penguins are not listed as a threatened species, it could be argued that management and conservation are unnecessary. However, some populations are under threat, particularly those located in urban and peri-urban areas of Australia. Little penguins also provide tourist opportunities at many sites around Australia (Dann *et al.* 1996) including the North West Coast of Tasmania where the populations are valued by local residents. Whilst many colonies of little penguins exist on offshore islands and generally away from terrestrial anthropogenic influences, most around the Tasmanian coastline are in peri-urban areas where the landscape has been

modified. Anthropogenic threats and associated predators, such as cats (*Felis catus*), dogs (*Canis familiaris*) and foxes (*Vulpes vulpes*), have been reported as taking eggs, chicks and adult birds (Stahel *et al.* 1987; Dann 1992).

Land degradation as a result of weed invasion, erosion, the use of coastal areas for recreation and strong storm surges is reducing habitat options for little penguins (Dann *et al.* 1992b; Fortescue 1995; Priddel *et al.* 2008). Traffic and rail mortality has been significant in Australia, particularly along the North West Coast where colonies occur adjacent to road and rail infrastructure. Installation of fences along much of the North West Coast has helped reduced little penguin mortality (A.Wind pers. comm.).

For seabirds, a scaled approach to planning could be a useful addition to conservation and management strategies. The spatial and temporal aspects of habitat scale can inform conservation and management issues related to the distribution of a species.

An overview of the approach adopted in this thesis is presented in Figure 1-3. This illustrates how spatial scale can be examined in the hierarchical distribution of a species. Each chapter focuses on a key aspect of each of the spatial scales of the organisation of little penguins.

Key factors operating at different habitat scales

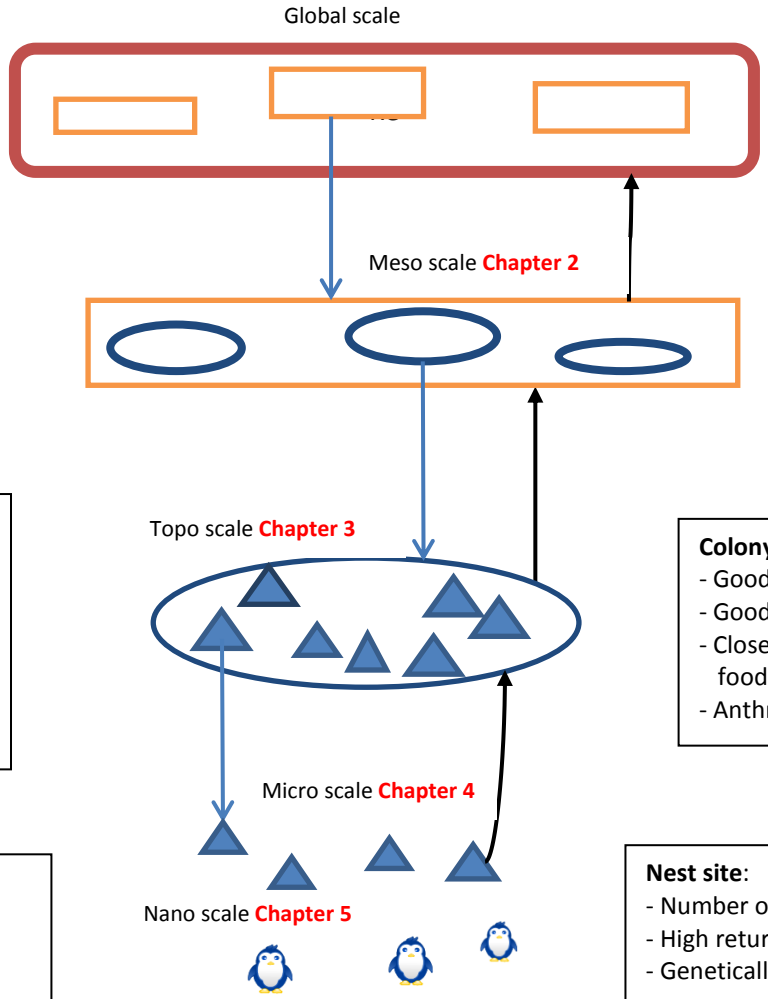
- Oceanographic factors
- Temporal changes in sea surface temperature / productivity
- Geographic landscape factors

- Proximity to foraging zones
- Spatial distribution of colonies
- Regional climate factors
- Human activities – fishing pressures

- Topographic variables
- Type of vegetation
- Predators
- Social interaction
- Use of colony by other species / interspecific competition
- Anthropogenic pressures
- Erosion / loss of habitat

- Types of burrows
- Microclimate - temperature, humidity
- Density dependent factors e.g. ecto parasites
- Fitness of individuals – natural selection

Habitat spatial scale



Successful indicators of persistence

Geographical zone:
-Persistence in regions over time of metapopulations

Regional geographical zone:
-Persistence of colonies over time

Colony:
- Good microclimate of burrow types,
- Good habitat characteristics
- Close proximity to food sources and sufficient food sources
- Anthropogenic pressures minimised

Nest site:
- Number of chicks fledging each year is high
- High return of adults to colony for future breeding.
- Genetically fit individuals

Figure 1-3 *Conceptual model of key factors operating at different habitat scales and what successful indicators may look like for a species. The habitat spatial scale is represented by the shapes; the top brown box represents the* global *distribution of a species (little penguin distribution in Australia and New Zealand); the next level represents the* meso *level represented by the regional distribution (the North - West Coast Tasmania study area of little penguins); the blue oval represents the* topo *scale represented by the colony (an example could be one of the six study colonies); the blue triangles represents the* micro *scale at the nest site (burrow) and at the* nano *scale the individual bird (penguin). The left hand side outlines the key factors that influence the habitat spatial scale, commencing with factors that have a large scale influence such as sea surface temperature at the geographic distribution of a species, to small local factors such as microclimate of burrows that influence survival of chicks at the nano scale. The right hand side provides the ideal indicators of persistence of a species at the different spatial levels commencing at the nest site and working back up to the geographic level. The scale of focus for each chapter is identified in the diagram.*

1.8 Research aims

The primary research aim of this thesis is to assess how the distribution of little penguins is affected by biophysical processes operating at different scales (*meso*, *topo*, *micro* and *nano*) at the regional, colony, and nest-site levels of organisation.

The specific objectives of this thesis are to:

(i) investigate the spatial distribution of penguin colonies at a variety of scales;
(ii) investigate the distribution pattern of nest-sites in a sample of colonies;
(iii) develop a habitat suitability model based on terrain variables that can predict the presence and absence of nest-sites;
(iv) investigate the thermal properties of various burrow types at micro temporal scales;
(v) investigate the relationship between the breeding success of little penguins and burrow type; and
(vi) consider these findings in a management framework for little penguins.

1.9 Framework of the thesis

The thesis is written as stand-alone papers, but cross references are made between chapters. All chapters, apart from Chapters 1 and 6 comprise a manuscript in preparation for publication. As a consequence, some overlap occurs with methods and context.

Chapter 2 focuses on the colonies and burrows of the little penguin breeding along the North West Coast of Tasmania. This chapter investigates the spatial distribution of penguin colonies at a variety of scales and the distribution pattern of nest-sites in a sample of colonies. The spatial relationships at different scales *meso* (statewide): 100s km, *topo* (colony): 10s km, and *micro* (within-colony): < 10m scales are examined to see whether the little penguin colony locations and nest-sites are clustered, random or dispersed. At the nest-site scale, the pattern analysis is extended to investigate what factors may contribute to the observed patterns.

Chapter 3 is a detailed study of six of the colonies from Doctor's Rocks to Sulphur Creek along the North West Coast. This chapter focuses on a combination of the spatial and non-spatial characteristics of the nest-sites of little penguins, with the objective of developing a habitat suitability model based on terrain variables that could predict the presence and absence of nest-sites.

Chapter 4 focuses on the *micro* scale, nest-site, and compares the thermal properties of various burrow types at micro temporal scales. This chapter investigates and quantifies the variation in temperature and relative humidity within each type. It also identifies the relationship between

the internal burrow temperature and outside ambient air temperature, and investigates whether burrow temperatures reach the Upper Critical Temperature (UCT) and if so, which categories of burrows are predisposed to reach the UCT.

Chapter 5 focuses on the *nano* scale and compares how the attributes of the various types of burrows impact on the chick production and the number of chicks in two sample colonies.

Chapter 6 synthesises the research and discusses the implications of the findings from a spatial scale perspective. This discussion explores the contribution this work makes to the study of a colonially breeding seabird develops new and novel approaches for the management and conservation of little penguins.

CHAPTER 2

Distributions of the colonies and burrows of the little penguin (*Eudyptula minor)* in Tasmania, at various scales

2 Distributions of the colonies and burrows of the Little Penguin (*Eudyptula minor)* in Tasmania, at different scales

2.1 Abstract

Many seabirds breed colonially. These colonies are usually positioned to minimise the distance to foraging grounds. Nest-site locations within a colony are a response to micro scale factors such as avoidance of predators or proximity to potential mates. Seabird colonies and the locations of nest-sites within them can show a clustered, random or dispersed pattern. In this study, spatial ecological analyses using GIS are undertaken at various spatial scales in order to understand how a series of little penguin (*Eudyptula minor)* colonies on the island of Tasmania and in particular the North West Coast region of the island are distributed along the coastline. In a peri-urban landscape little penguin colonies tend to be dispersed at the *meso* (geographical and regional) spatial scales. However, at the *micro* scale, nest-site locations within a colony are generally clustered, with high kernel density values in some patches within colonies. Nearest neighbour analysis indicates that the nest is influenced by the type of vegetation that the burrows are associated with. The distances between "vine type" (plants with long slender stems that trail or creep but need support) burrows are demonstrated to be significantly smaller than those between other burrow types. By examining the relationships obtained from spatial analysis, these results may provide some understanding of the densities within and among colonies that may have consequences for the conservation and management of little penguin colonies in areas where habitat is degraded.

2.2 Introduction

Spatial patterns can provide evidence of relationships between and among objects and their surroundings. In the field of ecology, spatial patterns may reflect intraspecific interactions that occur in a population and the results of the population's interaction with the habitat. The vast majority (95%) of seabirds form colonies for breeding and moulting in a variety of habitats (Wittenberger & Hunt Jr 1985; Schreiber & Burger 2001). These colonies can be distributed quite widely in a geographic zone or landscape but their location usually depends on proximity to foraging areas, or other factors such as protection from predation (Buckley & Buckley 1980) or providing suitable conditions for take-off or access to colonies (Schulz *et al.* 2005). Space is required for either surface or burrow nests, for which seabirds may have to compete with their neighbours. Hereafter in this chapter, "nest-site" is used to describe both burrows and surface nests.

In the context of seabirds, a colony has been described as a group of individual organisms that live close together at a breeding site and maintain that association to an extent that is greater than what would be expected by chance (Coulson 2001). The adaptive significance of colonial breeding and the impact it has on the location, foraging and size of colonies in a geographic region has been the subject of much research (Ashmole 1963; Lack 1968; Wittenberger & Hunt Jr 1985; Ainley *et al.* 2003; Dann & Norman 2006) and controversy (Kharitonov & Siegel-Causey 1988; Siegel-Causey & Kharitonov 1990). It has been suggested that competition within and among neighbouring colonies modifies the distribution and size of colonies (Furness & Birkhead 1984). However, it remains unclear what creates or defines the boundaries of a colony. Also, when do interacting groups of birds cease interaction so that they can be considered separate colonies or subgroups of a single larger colony? It could be that colonies within close proximity to each other are part of a metapopulation and what appear to be discrete and possibly independent colonies may in fact be linked by dispersal (Newton 1998) or connectivity (Harrison & Hastings 1996). A metapopulation is generally considered to consist of several spatially separated populations of the same species within areas of suitable habitat in a patch network (Hanski 1998; Schippers *et al.* 2009).

Landscape features enable a species to be comprised of more or less isolated subpopulations (Newton 1998). Whilst the reasons for colony site selection are difficult to establish, it is possible to examine the distribution of colonies within a landscape. New colonies can form when only poor habitat for nest-sites remains in old colonies, and consequently the growth of new colonies, even in sub-optimal habitat, can exceed that of old colonies by attracting prospective new breeders e.g. black-legged kittiwakes *(Rissa tridactyla)* (Kildaw *et al.* 2005). Intense foraging around a colony can lead to a decrease in food supply, particularly during the breeding season when demand for food is high, an effect known as Ashmole's Halo. This results in a decrease in breeding success and consequently a regulation of colony size due to the intraspecific competition for food and breeding sites (Ashmole 1963). Variations to Ashmole's model include the "hungry horde" model whereby the size of the colony is inversely related to the number of conspecifics using common feeding grounds; or the "hinterland" model, where seabirds forage more in areas closest to the colony (Cairns 1989, 1992). Further, the location of foraging zones has been identified as the determining factor for colony position, causing, for example, large colonies to occur further apart than expected by chance (Furness & Birkhead 1984; Forbes *et al.* 2000). In a study of four species of seabirds, it was found that where neighbouring colonies shared common foraging zones, birds from larger colonies depleted resources, causing a reduction in size of smaller neighbouring colonies (Furness & Birkhead 1984).

Different species of seabirds appear to respond differently to population regulation, with two types of patterns being described by Dann et al (2006) and references therein. Colony size of black-legged kittiwakes (*Rissa tridactyla*) decreased with the quality of the foraging grounds. A density-dependent hinterland model was proposed for gannets *(Morus bassanus)* suggesting that foraging ranges increase as a result of increase in density of neighbouring colonies due to decreasing local prey availability (Wakefield *et al.* 2013) . A combination of available breeding area and intraspecific competition for food may determine the population size of little penguins (*Eudyptula minor)* (Dann & Norman 2006).

Little penguins forage within 20 km from the coast and when foraging to feed young they can undertake trips up to 30km from their colony (Collins *et al.* 1999; Hoskins *et al.* 2008). Colony distribution may therefore be influenced by not only the presence of foraging areas, but also suitable characteristics of the landscape, resulting in clustered, dispersed or randomly distributed colonies along the coast. At a *micro* scale, the distribution of nest-sites within a colony may be the result of a reproductive imperative where the nest distribution reflects the requirements of the birds during the breeding season or protection from predators. Accordingly, a hierarchy of factors may operate at different spatial and temporal scales on the location of colonies and nest-sites within the colony.

Understanding the spatial factors that influence colony size, density and distribution of nest-sites can contribute to an understanding of how seabirds can survive in their habitat. This is particularly the case in the peri-urban environments, due to the additional pressures caused by close proximity to human infrastructure and disturbance. The use of geographic information systems (GIS) as a tool to describe, analyse, and predict suitable habitat characteristics, and understand the spatial aspects of habitat selection of plants and animals is increasing (Bergin 1992; Guisan & Zimmermann 2000; Morrison *et al.* 2006; Bricher *et al.* 2008; Franklin 2009). Geographic information systems have already been used for extracting habitat and location variables to predict density of breeding burrows in sooty shearwaters *(Puffinus griseus)* and mottled petrels *(Pterodroma inexpectata)* (Scott *et al.* 2009).

Geographic Information Systems (GIS) have only been used to investigate the spatial point pattern distribution of nest-sites of penguins on land. Point pattern analysis of nests within a colony of blue penguins in New Zealand showed that burrow habitat type did not appear to influence the breeding success and there was no significant difference in breeding success between colonial and isolated breeders in either study area (Braidwood *et al.* 2011). Productivity in some habitat types may not be greater due to higher density of nests per unit area. Even so, it should be recognised that GIS is only as useful as the data available and much

of that is determined by the accuracy of the data collected by a Global Positioning System (GPS).

This study focuses on the colonies and burrows of the little penguin, a burrowing seabird that is distributed around southern Australia. In Tasmania, little penguin colonies are found around the coastline and on many offshore islands. Very little documented information existed on the distribution of little penguin colonies in Tasmania and its surrounds before 1990. Penguin colonies had previously been noted on the Bass Strait Islands, East Coast Islands, South Coast Islands and at Stanley, Doctor's Rocks, Somerset and some in the Hobart region (Marchant & Higgins 1990). Surveys undertaken between 1987 -1997 showed that little penguins were present on all of the offshore islands, but due to their nesting habits they were difficult to count (Brothers *et al.* 2001).

Considerable decreases in populations of little penguins in South East Tasmania have been documented (Stevenson & Woehler 2007). Population pressures included increasing urban development, introduced vertebrates, and modification rendering the habitat unsuitable for penguins. No long term records of little penguins in North West Tasmania (the site of this study) are available. Low numbers of little penguins were recorded west of Sisters Hills and Rocky Hills, Tasmania in 1918, (Fletcher 1918), however this colony no longer exists. The number of colonies along the North West Coast Tasmania has been known to vary with anecdotal information, suggesting a loss of, or decrease in, a few colonies due to introduced predators (dogs and cats), habitat degradation and decrease in available habitat.

Clustering of nest-sites in certain areas may indicate that there is some combination of variables that is favourable for the formation of nests or burrows. However, in many cases, the expansion of colonies inland has been constrained by coastal development and transport infrastructure. Proximity to human settlements means that potential predators such as cats and dogs may have access to nesting areas. Consequently, as penguins have to forage for food during the day, there may be strong pressure by parents to find the best protection for their young under cover, which may increase the survival of chicks, possibly resulting in highly clustered areas.

The aim of the study is to investigate the spatial distribution of penguin colonies at a variety of scales and to determine the distribution pattern of nest-sites in a sample of colonies. The spatial relationships at different scales: *meso* (state-wide: 100s km), regional (colony: 10s km); *coarse* (nest-site distribution within colonies: 100s m) and *micro* (nest-site characteristics: < 1m), are examined to see whether their locations are clustered, random or dispersed. At the nest-site *micro* scale (nest-site), the pattern analysis is extended to investigate what factors may

contribute to the observed patterns. Six colonies from Doctor's Rocks to Sulphur Creek along the North West Coast of Tasmania are used.

The specific aims and associated null hypotheses (Ho) of the study were to:

1) investigate the dispersal pattern of penguin colonies around the coast of Tasmania
   Ho: colonies are distributed randomly around the coast
2) identify and compare the distribution of active nest-sites within and among colonies and test for departures from randomness of placement of burrows within the colony.
   Ho: nest-sites within a colony are distributed randomly
3) examine how knowledge of spatial scales of colonies can be applied to management of penguin colonies.

2.3 Methods

2.3.1 Data Collection

2.3.1.1 Hierarchy of spatial scale for analysis

Statewide level (Meso scale)

A map of Tasmania with little penguin colonies identified across the State was obtained from the Land Information System Tasmania web-based portal (www.theLIST.tas.gov.au). This geographic layer consisting of point locations of little penguin colonies across the state, was established in 1999 following the Iron Barron oil spill (Goldsworthy *et al.* 2000) and updated in 2003 by a combination of a survey and anecdotal information. The point data in a small number of places had limited accuracy, as some locations had been extracted from hand drawn maps, which may have introduced error) through the digitising process. As locations of colonies were being analysed, the presence of populations greater than ten birds were extracted from the data. The perimeters of many colonies around the state were unknown so every colony was represented as a point on the map at its location.

Regional level- North West Coast (Meso scale)

The perimeters of six study colonies were mapped using a differential GPS (DGPS) Promark 3, whilst the perimeters of the other colonies were digitised from known extents using a combination of aerial photographs and local landscape knowledge from Wynyard to Devonport. Accuracy at this level of the digitised colonies was approximately ± 10m in the horizontal plane.

Colony level (Topo scale)

For the colony investigation, the study area was located along the North West Coast of Tasmania. Detailed mapping of sections of the following six colonies was used in this study: Cooee Point (-41.00ºS 145.87ºE), Doctor's Rocks (-41.00ºS 145.77ºE), Ocean Vista (-41.03ºS 145.86ºE), Parsonage Point (-41.04ºS 145.89ºE), Sulphur Creek (-41.00ºS 146.02ºE) and Woody Point (-41.03ºS 145.80ºE). These areas were selected to provide a range of habitat types, based on vegetation. A colony was defined here as being a contiguous patch where burrows are located within 5 m of each other. Fieldwork was undertaken during the breeding seasons from December – March in 2008/2009, 2009/2010 and 2010/2011 when the presence of birds in the colonies was at its peak. A breeding season was defined as when birds start laying and incubating eggs, and raising chicks. The peak activity occurs during December to January. Locating nest-sites is easier, during this period due to the increased presence of scats, feathers, footprints and the smell of chicks.

2.3.1.2 Differential GPS

Output accuracy is only as good as input data and tools used in the process. .The use of DGPS provides better accuracy and precision in recording the placement of a location (such as a nest-site) in the landscape than a handheld GPS, or earlier approaches such as mapping points onto an arbitrary grid. The horizontal accuracy of the DGPS used is 20 cm which is better than the 5-10 m obtained from most handheld GPS. The DGPS is also more reliable as it less prone to outliers. This reliability was obtained by use of a local base station and transmission to a rover in real time which improved the user position (Appendix 1). Also, using a 1 m DEM means that the pixel sizes (1 m x 1 m) produces better height quality than lower resolution 5 m DEM. Consequently had GPS data been combined with a 1 m DEM points may have been placed up to 5m away resulting in a different height, depending on the terrain. It was expected that using a lower quality GPS (i.e. handheld GPS) would have produced lower quality results.

A point pattern analysis (PPA) is most effective when all points in an area are mapped. This is a time-consuming process that is not often completed. In order to make this possible, Real-Time Kinematic (RTK) surveying using Global Navigation Satellite Systems technology (GNSS) was used to map the nest-site locations as this provides at least 20 cm accuracy. The ProMark 3 single-frequency RTK Differential GPS (DGPS) system used two GNSS antennae, with one a static point at a known location referred to as the base station (Figure 2-1a) and the other attached to a backpack on the recorder known as the rover (Figure 2-1b). Single-frequency RTK mapping is a relative positioning technique which measures the position of the two antennae relative to each other in real time.

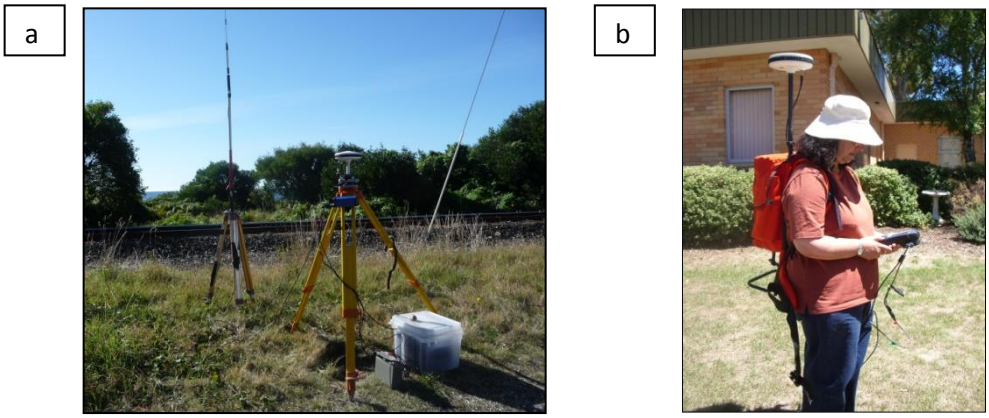


Figure 2-1 *Differential GPS set up in the field. a): Base station set up; b) Rover used in the field to log burrow points.*

The following protocol was used:

1 The base station which was in close proximity to each colony had a clear sky view. There were minimal surrounding obstructions and the transmitting radio antenna was positioned as high as possible. Once the base station had been collecting data over a known point for a minimum of 5 h, the data were transmitted as a Receiver Independent Exchange Format RINEX file to the Precise Point Positioning (PPP) online service operated by the Geodetic Survey Division of Natural Resources Canada called CSRS-PPP (http://webapp.geod.nrcan.gc.ca/geod/tools-outils/ppp.php) in order to obtain the position of the base station.

2 Locations of nest-sites were only recorded when there was a minimum of six satellites available. In 90% of cases a signal was received from nine or more satellites. All satellite signals were received from an angle of at least 10^0 above the horizon and the positional dilution of precision (PDOP) of > 99% of the readings was < 3. Positional dilution of precision values measure data quality in regards to the geometry of the satellites in view; a value of < 3 is considered excellent and indicates high precision. In 0.6% of the readings, the PDOP was between 4 and 5 (Table 2-1) which is still in the "good" range. Locations were recorded every second and averaged over 20 s. All mapping of nest locations was conducted in UTM WGS84 Zone 55.

3 The rover data were downloaded via Mobile Mapper and converted to shape files for analysis in ArcGIS 10.

Table 2-1 *The mean and standard deviation (SD) of the positional dilution of precision (PDOP) of the colony locations recorded for little penguin nest-sites. All colonies show mean PDOP < 3, which indicates the readings are of very high quality. The high number of satellites also increases accuracy of GPS signals.*

Colony	Number of burrows	PDOP		Average number of satellites
		Mean	SD	
Cooee Point	107	1.66	0.31	10.13
Doctor's Rocks	727	1.77	0.35	9.92
Ocean Vista	137	1.48	0.31	10.91
Parsonage Point	335	1.66	0.26	10.30
Sulphur Creek	270	1.77	0.40	9.33
Woody Point	93	1.52	0.18	11.26

2.3.1.3 Nest-sites

Complete (or sections of) colonies were mapped in four out of the six colonies studied (Cooee Point, Ocean Vista, Parsonage Point and Woody Point) as they were small colonies, whereas large sections of Doctor's Rocks and Sulphur Creek colonies were mapped. In all cases burrows were mapped after exhaustive searching. A nest-site was defined as a hollow in vegetation where penguins nest on the surface using vegetation as a cover, or a burrow where penguins dig under the soil surface or other substrate, such as rocks. Both were treated as a nest-site and were identified because of the presence of scats, feathers, tracks or smell. A very distinct fishy smell could be detected when chicks were present in the burrows. Only nest-sites that were currently being used by penguins were recorded.

Nest-sites were tagged with pink flagging tape as they were found. The searching process was repeated once in order to make sure no active nest-sites were missed on the first pass. Nest-site locations were then logged using the Promark 3 units. The recording of each burrow involved standing at the entrance and logging the point for a minimum of 20 s to ensure correct positioning. The burrow type of each nest-site was concurrently recorded in a field book.

Burrow type

The burrow type was defined by the material that formed the roof of the nest-site. For example, where nest-sites were dug into sand and had a sand roof they were identified as a sand burrow, but where they had a sandy floor but were covered in vegetation they were characterised by the specific type of the vegetation. The vegetation was classified using the CSIRO handbook (Hnatiuk 2009). This uses the National Vegetation Information System (NVIS) framework (ESCAVI 2003) (Table 2-2). Figure 2-2 provides examples of four of the burrows mapped.

Table 2-2 *Burrow classification system showing examples for each category. See Appendix 1 for a full list of vegetation species identified in the study sites*.

Classification categories of burrow types	**Examples**
Artificial	Black plastic pipe, concrete pipes or slabs, tyres, concrete igloos
Grass	Knobby club sedge *Ficinea nodosa*, Marram *Ammophila arenaria,* Onion weed *Asphodelus fistulosus*, Rush *Juncus* sp., Sagg *Lomandra longifolia*, Sedge *Carex* sp., Tussock grass *Poa* sp.
Herb	Buzzy *Acaena* spp, Fire bush *Senecio prenanthoides*
Non Vegetation (Minerals)	Rock, sand or soil
Shrub	African boxthorn *Lycium ferocissium*, African daisy *Arcotis stoechadofolia*, Coastal boobyalla *Myoporum insulare*, Coastal saltbush *Rhagodia candolleana*, Coastal wattle *Acacia longifolia var. sophorae*, Correa *Correa alba*,
Tree	Pine *Pinus radiata*, Swamp paperbark *Melaleuca ericifolia*
Vine*	Bower spinach *Tetragonia implexicoma*, Cape ivy *Delirea odorata*, Honeysuckle *Lonicera periclymenum*, Periwinkle *Vinca major*, Pigface *Carpobrotus* sp., Rambling dock *Acetosa sagittata*
Wood	Logs, Branches
Fern	Bracken *Pteridium esculentum*

Vine* plants with long slender stems that trails or creeps but need support.

Figure 2-2 *Four types of burrows that were mapped and found in all colonies on the North West Coast of Tasmania:a) Artificial, b) Grass, c) Vine, d) Sand*.

2.3.2 Data processing and analysing methods

2.3.2.1 Digital Elevation Model

A digital elevation model (DEM) is a baseline data layer used in a GIS environment (Guisan & Zimmermann 2000), and is a raster representation of a continuous surface. The accuracy of the data is determined primarily by the resolution (distance between two points); the higher the resolution of the DEM, the more fine-scale features can be captured and used in analysis. The DEM used in this study was based on LiDAR (airborne laser scanning) point data produced for the ACE CRC Climate Futures project in 2008. The DEM has a 1 m × 1 m pixel resolution in the horizontal and vertical planes. It was supplied via the Information and Land Services Division (ILS) of the Department of Primary Industries, Parks, Water and Environment (DPIPWE). Data was captured in WGS84 and converted to GDA 94. All layers were projected in GDA94 MGA zone 55. A second order derivative, *hillshade* was also developed from the 1 m DEM.

A series of GIS processes were undertaken at each hierarchy of scale using the colony data at the state and regional level; and the burrow data at the colony and intra colony level (Table 2-3).

Table 2-3 *Summary of processes used in pattern analysis at each spatial scale of habitat*

Scale of investigation	GIS processes used	Point or polygon
Statewide level ***Meso* scale**	Average Nearest Neighbour (ANN)	Point (colony) along coast of Tasmania
Regional scale ***Meso* scale**	Average Nearest Neighbour (ANN)	Polygons (colony) along the NW coast
Colony level ***Coarse* scale**	Average Nearest Neighbour (ANN) Perimeter / Area ratio (P/A)	Points (burrows) within the colony
Intra colony ***Micro* scale**	Average Nearest Neighbour (ANN) Kernel Density Nearest neighbour	Points (burrows) within the colony and cluster associations to burrow type

An outline of each of the GIS processes follows.

Average Nearest Neighbour (ANN)

The Euclidean distance was used with the Average Nearest Neighbour index (ANN) method to analyse the distance between each feature and its nearest neighbour. The ANN index is based on measuring the distance between the feature centroid and its nearest neighbour centroid location (Mitchel 2005). The average of all these features was then calculated and compared to the average distance for a hypothetical random distribution. If the average distance was small compared to a hypothetical random distribution then the features were considered clustered (Mitchel 2005). This GIS tool was used to test the null hypothesis that little penguin colonies are randomly distributed around the coastline of Tasmania. To calculate the ANN ratio, a buffer of 500 m was used on the inside of the coast line to ensure all burrows on the coast were constrained by the buffer. The buffer inland from the coast was used to simulate the extent of the distance that penguins could traverse to reach a colony and consequently constrained the ANN ratio to within the coastal area. The area of this coastal strip was then used in the calculation of the ANN ratio. This process was used at three habitat spatial scales (Table 2-3). To calculate the ANN ratio of the colonies in the North West Coast of Tasmania, the polygons were converted to points and then analysed. The ANN ratio indicated if the distribution was clustered dispersed or random. Additionally Z values indicated the percentage likelihood of the distribution occurring. A negative Z value indicated clustering of burrows whilst a positive Z

value indicated a dispersed pattern. Larger negative or positive numbers indicated the burrows were more highly clustered or dispersed respectively in the colony.

Kernel density

Kernel density was used to estimate the density around each burrow within its neighbourhood and indicated where the density was concentrated by using the quadratic kernel function (Silverman 1986). The kernel density analysis was applied to all the colonies as one input layer so that the surface obtained could be compared between and among colonies to determine which had the densest surfaces. Isopleths (90%) were drawn to represent the boundary lines containing a specified proportion of the surface. Aerial photographs used in the maps were obtained from the Land Information System Tasmania web-based portal (www.theLIST.tas.gov.au).

Nearest neighbour

The nearest neighbour, a first order analysis, calculates the nearest neighbour of any one point. In many examples, interactions between and among objects exist, so that nearest-neighbour distances are not randomly distributed. Edge effects are not affected by this measurement as actual nearest distance between objects was measured, which was not dependent on the perimeter of the area (Diggle 1983). A table was generated which identified the nearest neighbour for each burrow point. This was then analysed using the statistical programming language in R (R Core team 2013) and *lme* function (package *nlme*). A linear mixed model was used to investigate the nearest neighbour distance between burrows (response variable), which was fitted with REML, burrow types (*Burrow Type*) as the fixed term and colony (*Location*) as the random term.

Model: *Nearest neighbour distance. ~ Burrow Type +1|Location*

The significance of the results was investigated using ANOVA and Post hoc Tukey test.

Perimeter / Area ratio (P/A)

One aspect of shapes that can be investigated at is the Perimeter /Area ratio (P/A) which reflects the area and shape of the colony. The perimeter and area were calculated in the GIS environment using the boundaries of the colony that contained the burrows mapped. The boundaries of the sampled colony were defined as either the vegetation edge on the coastal front, the fence or infrastructure on the inland side. This ratio provided a measure that was used to compare the colonies.

2.4 Results

2.4.1 State level (*Meso* scale)

Figure 2-3 shows 112 records of little penguin colonies (i.e. >10 birds) along the coast of Tasmania, which represents only 29% of total records of little penguins from the on-line databases. Many of the remaining records of little penguins were from offshore islands and others were of single sightings of penguins on land. Extreme caution was used in interpreting these data. While they can indicate the distribution of little penguin colonies, the data did not give any indication of size or area of the colonies, and many of the colonies may no longer be in existence, given the time since the observations were recorded.

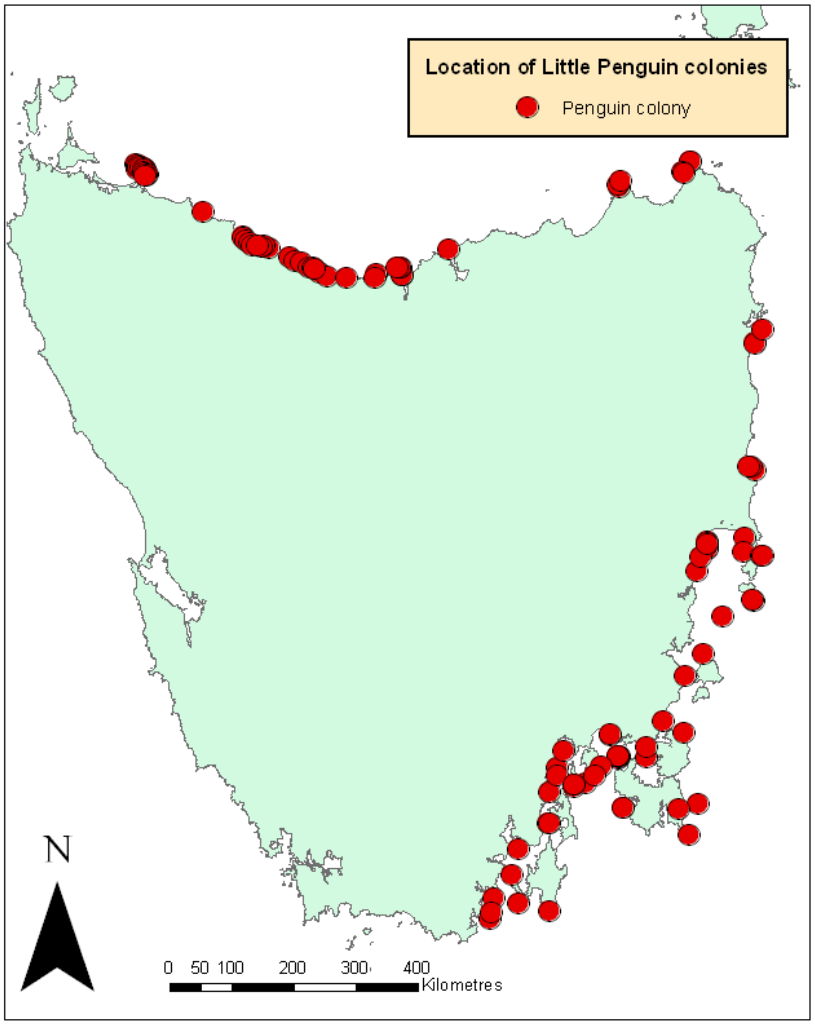


Figure 2-3 *Map showing records of little penguin colonies (nominally >10 birds) around the coastline of Tasmania, based on data from the LIST. The locations exclude many of the islands where penguins can breed. The accuracy and precision of many of these data are unknown.*

Based on these data, little penguin colonies appear to be absent from the very tip of the North West Coast and along the West Coast of the Tasmanian coastline (Figure 2-3). Current anecdotal information indicates that there is some presence of penguins in these areas (but the sizes of these colonies are presently unknown). The aforementioned absence may therefore simply reflect an absence of records. These colonies are outside the study range, but their presence would more than likely add to the distribution of colonies along the coast. Also there are many offshore islands that show the presence of little penguins that are not shown on the map.

The ANN ratio of 1.303, and Z score of 5.86 ($p<0.001$) for these data, indicates a dispersed distribution of colonies around the Tasmanian coastline. There is < 1% likelihood that this dispersed pattern could be the result of chance.

2.4.2 Regional level (*Meso* scale)

The colonies analysed in this section were located from Devonport to 12 km west of Burnie (Figure 2-4). The ANN ratio of 1.446, and Z score of 3.718 ($p<0.001$) for these data, indicates a dispersed distribution of colonies in this region. There is< 1% likelihood that this pattern could be the result of chance.

A closer examination of the colonies in Figure 2-3 suggests that identifying the 17 patches as separate colonies in a total distance of 50 km may not be justified. If the proximity of the colonies is measured using Euclidean distance, 13 of the 17 colonies (76%) are < 2 km apart (Table 2-4).

Table 2-4 *Inter-colony distance (measured as a Euclidean distance between the western end of one polygon and the eastern end of the next colony polygon along the coast) for little penguin (Eudyptula minor) colonies.. For instance, the distance between colony 1 and 2 is 1.95 km. Number of colonies based on spatial scales of independence is suggested. *Named colonies are used in further analysis.Spatial scale of independence provides another method of examining possible numbers of colonies present. Three suggested distances are proposed for areas to be considered distinct colonies; greater than 2.0 km, greater than 1.0km and greater than 0.5 km.*

Colony number	**Inter colony distance (km)**	**Possible colonies based on spatial scale of independence of > 2.0 km**	**Possible colonies based on spatial scale of independence of > 1.0 km**	**Possible colonies based on spatial scale of independence of > 0.5 km**
1* Doctor's Rocks	1.95	1	1	1
2* Woody Point	3.04	2	2	2
3	0.70	3	3	3
4* Ocean Vista	0.50			4
5* Cooee Point	1.87		4	
6* Parsonage Point	8.30	4	5	5
7 * Sulphur Creek	1.40	5	6	6
8	0.80		7	7
9	1.00			8
10	2.20	6	8	9
11	0.70	7	9	10
12	0.20			11
13	0.70			
14	0.60			12
15	1.38		10	13
16	9.60	8	11	14
17				

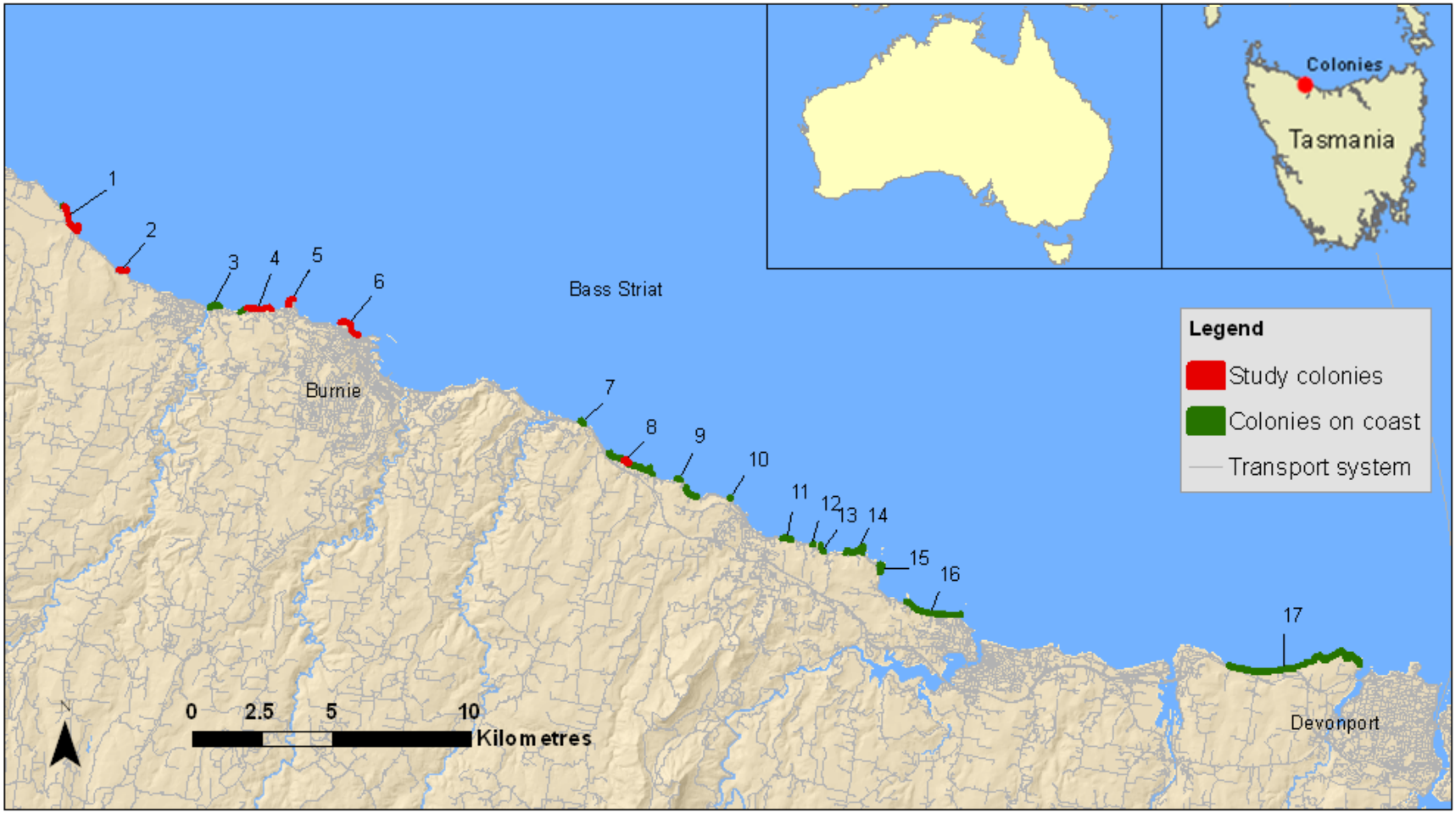


Figure 2-4 *Location of North West Coast little penguin colonies. The study colonies in red are: 1: Doctor's Rocks, 2: Woody Point, 4: Ocean Vista, 5: Cooee Point, 6: Parsonage Point, 8: Sulphur Creek*

2.4.3 Colony level (*Topo* scale)

The six study colonies located in peri-urban areas with their inland extent clearly constrained by infrastructure. The colonies were elongate, with the width of habitat ranging from a minimum of 4 m at Ocean Vista to a maximum of 87 m at Sulphur Creek. The Perimeter/Area (P/A) at Ocean Vista of 0.2 indicated an elongate and narrow colony, Sulphur Creek P/A of 0.05 indicated a more rectangular shaped colony (Table 2-5).

Overall, the density of penguin nests was calculated by dividing the area of the colony polygon by the number of active nest-sites. Densities ranged from 0.01 – 0.02 nest-sites m^{-2}, and are very similar in all colonies (Table 2-5). This measure does not indicate whether density of burrows varies within a colony.

The pattern of nest-site distribution varied among the colonies. Three of the colonies, Doctor's Rocks, Parsonage Point and Sulphur Creek, showed clustering of burrows with ANN ratios < 1 and Z scores < -1.65, whilst Woody Point and Ocean Vista demonstrated dispersion of little penguin nest-sites (ANN ratio > 1.65) (Table 2.6). Nest-sites at Cooee Point were randomly distributed with ANN ratio 0.96 and Z score -0.86. This result may be an artefact however, as the majority of nest-sites were artificial and their location was anthropogenically determined.

2.4.4 Intra colony level (*Micro* scale)

2.4.4.1 Kernel Density

Figures 2-5 – 2-10 show the nest-site locations in the colony, plus kernel densities of each colony. The search radius was 10 m, with output cell size of 1 (equivalent of the 1 m cell grid size of the DEM). The highest kernel density (0.12 - 0.16) was found in patches in three of the colonies viz Doctor's Rocks, Parsonage Point and Sulphur Creek; the three deemed to be clustered. A single very small patch of high kernel density can also be seen in the Ocean Visa colony (Figure 2-6).

2.4.4.2 Nearest neighbour analysis

The nearest neighbour (NN) was identified for all nest-sites in each colony and the majority of the burrows were within 5 m of each other amongst all colonies (Figure 2-11a). One burrow was identified in Cooee Point colony with a NN of 17.0 m, the maximum NN distance recorded in the analysis. Whilst this might suggest an isolated burrow, it might also suggest that no other nest-sites in the area were used at the time of mapping. Some variations existed among the colonies (Figure 2-11b), the maximum distance between burrows peaked at 2 m in the Doctor's Rock's and Parsonage Point colonies.

Table 2-5 *Summary characteristics of six study coloniesof little penguins. The largest sample colony in the study was Doctor's Rocks and the smallest Cooee Point. Area and perimeter values calculated from the polygons of the study areas in GIS were used to calculate the Perimeter/Area (P/A) ratio. This provides a relative comparison of the shape of the colony, with higher values tending to indicate a long thin shape compared to slightly lower values which are wider. Density of burrows indicates the highest density was obtained in the Cooee Point colony*.

Colony name	Location (Lat long)	Description of colony	Study area in colony (m^2)	Perimeter to area ratio (P/A)	Number of burrows	Estimated number of pairs of little penguins *	Density of burrows (m^{-2})
Cooee Point	-41.00°S 145.87°E	Old disused land with mostly artificial burrows added to supplement rock burrows. Patchy vegetation.	6663	0.13	107	94	0.016
Doctor's Rocks	-41.00°S 145.77°E	Coastal reserve area with a mixture of varying vegetation and burrow types	42733	0.06	727	664	0.017
Ocean Vista	-41.03°S 145.86°E	A very narrow strip of coastal vegetation with a mixture of varying vegetation and burrow types	9894	0.20	137	117	0.014
Parsonage Point	-41.04°S 145.89°E	Colony sited on reclaimed land previously used as building tip site. Coastal vegetation re-established and artificial burrows supplement the area.	17663	0.08	335	305	0.017
Sulphur Creek	-41.00°S 146.02°E	Colony sited on the coastal foreshore with dense cover of weeds.	14526	0.05	270	267	0.019
Woody Point	-41.03°S 145.80°E	A small patch of land sited near a sewage treatment plant with mixed vegetation.	7340	0.13	93	92	0.013

* An assumption was made that all active burrows indicated a pair of little penguins. This may have resulted in an overestimate of the numbers presented here.

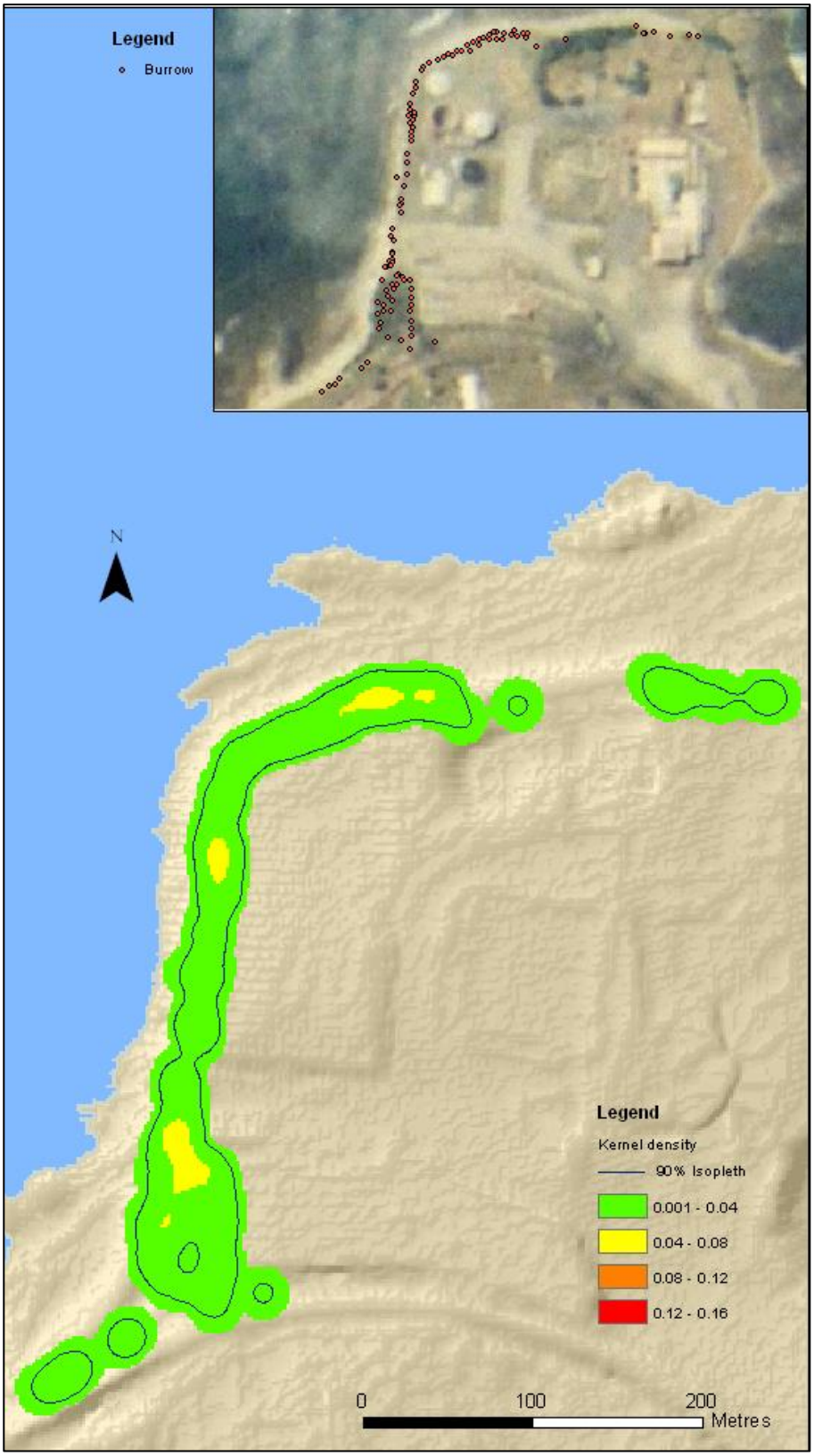


Figure 2-5 *Cooee Point little penguin colony. Kernel density plot with absence of the higher density values present in other colonies. The majority of burrows are artificial nests in this colony. The inset shows the burrow locations.*

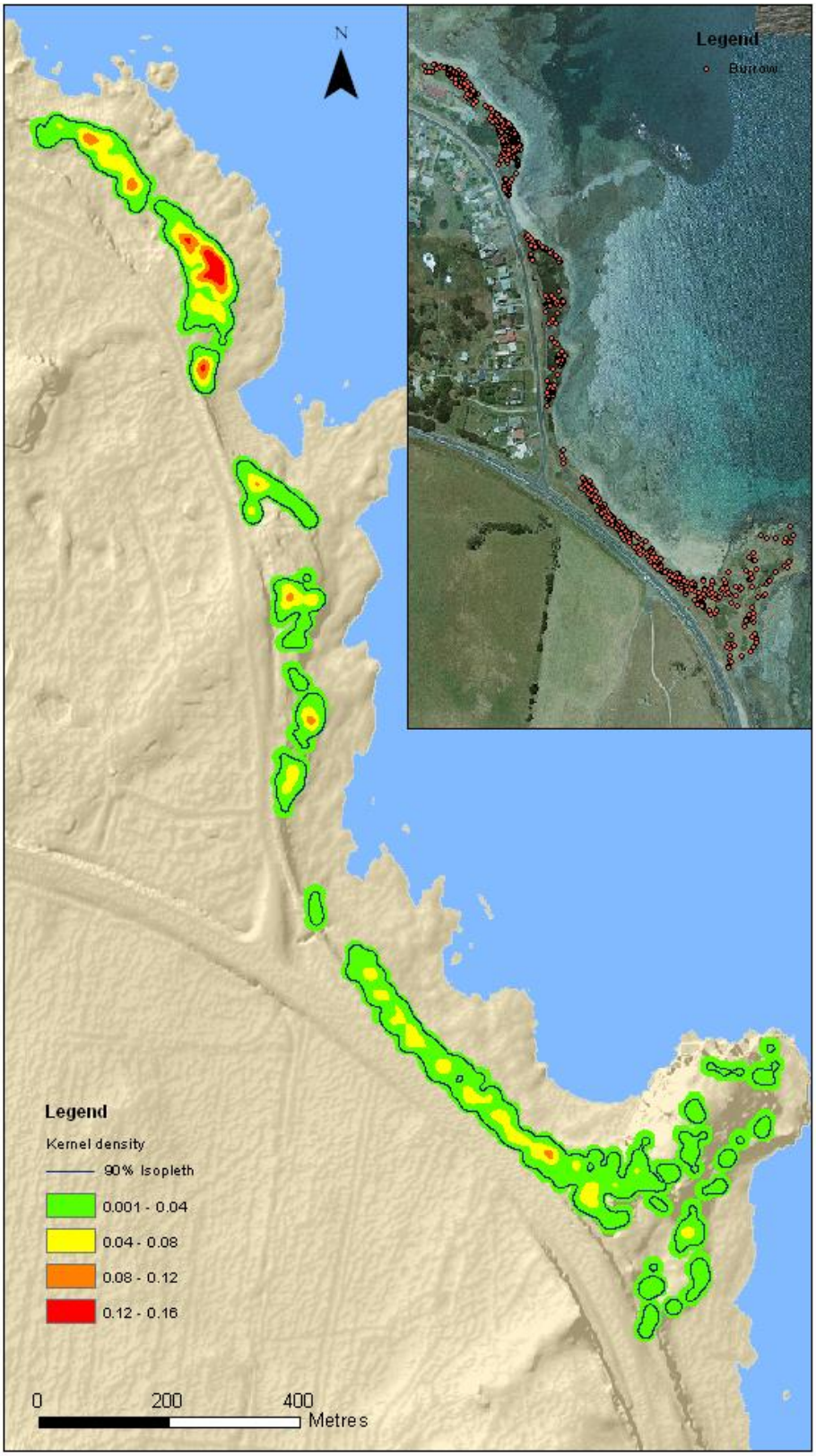


Figure 2-6 *Doctor's Rocks little penguin colony. Kernel density plot with a higher density illustrated in red in a few small patches in the sampled area. The inset shows the burrow locations.*

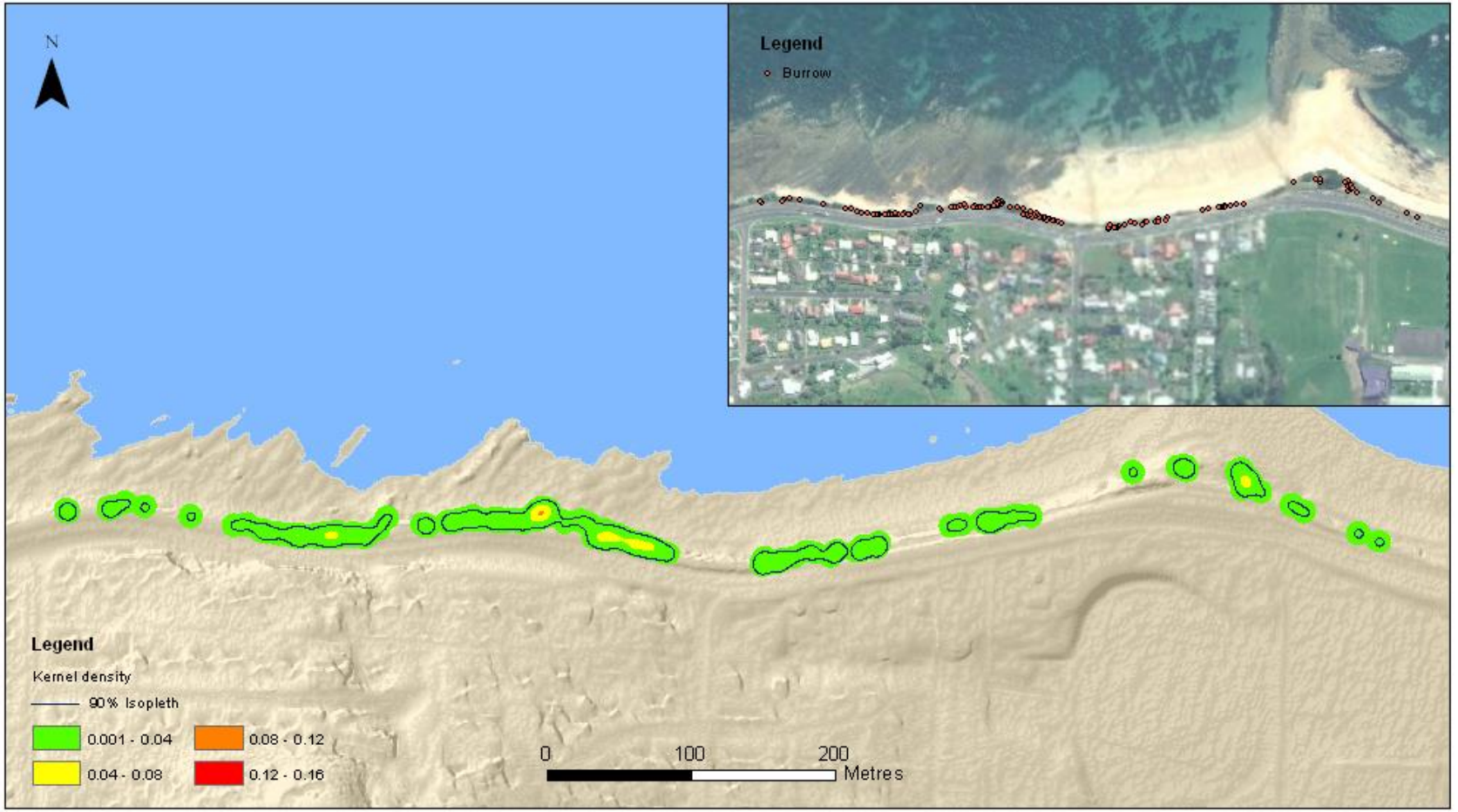


Figure 2-7 *Ocean Vista little penguin colony. Kernel density plot with a higher density illustrated in red in two small patches in the sampled area. The inset shows the burrow locations.*

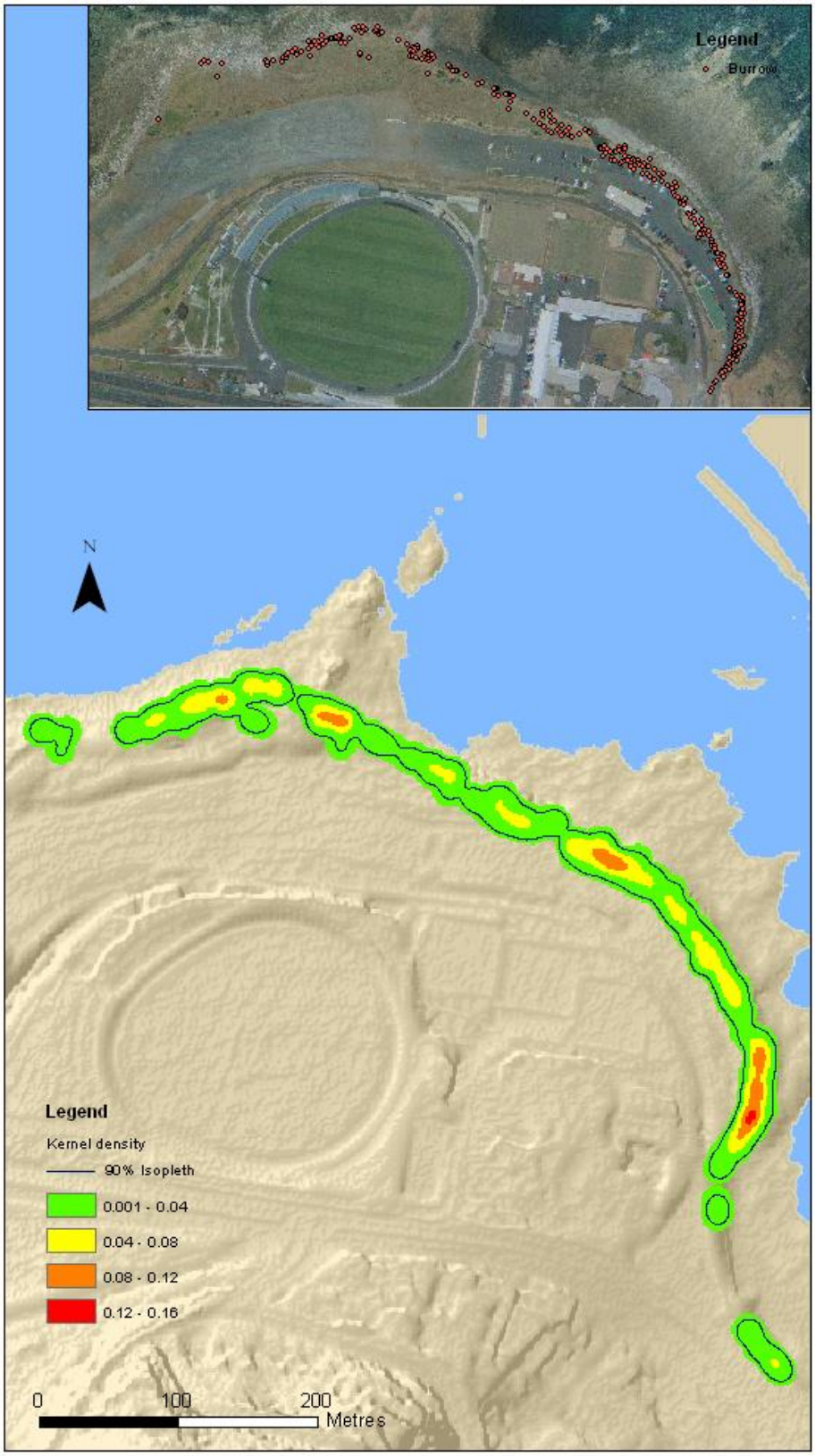


Figure 2-8 *Parsonage Point little penguin colony. Kernel density plot with a higher density illustrated in red in four patches in the sampled area. The inset shows the burrow locations.*

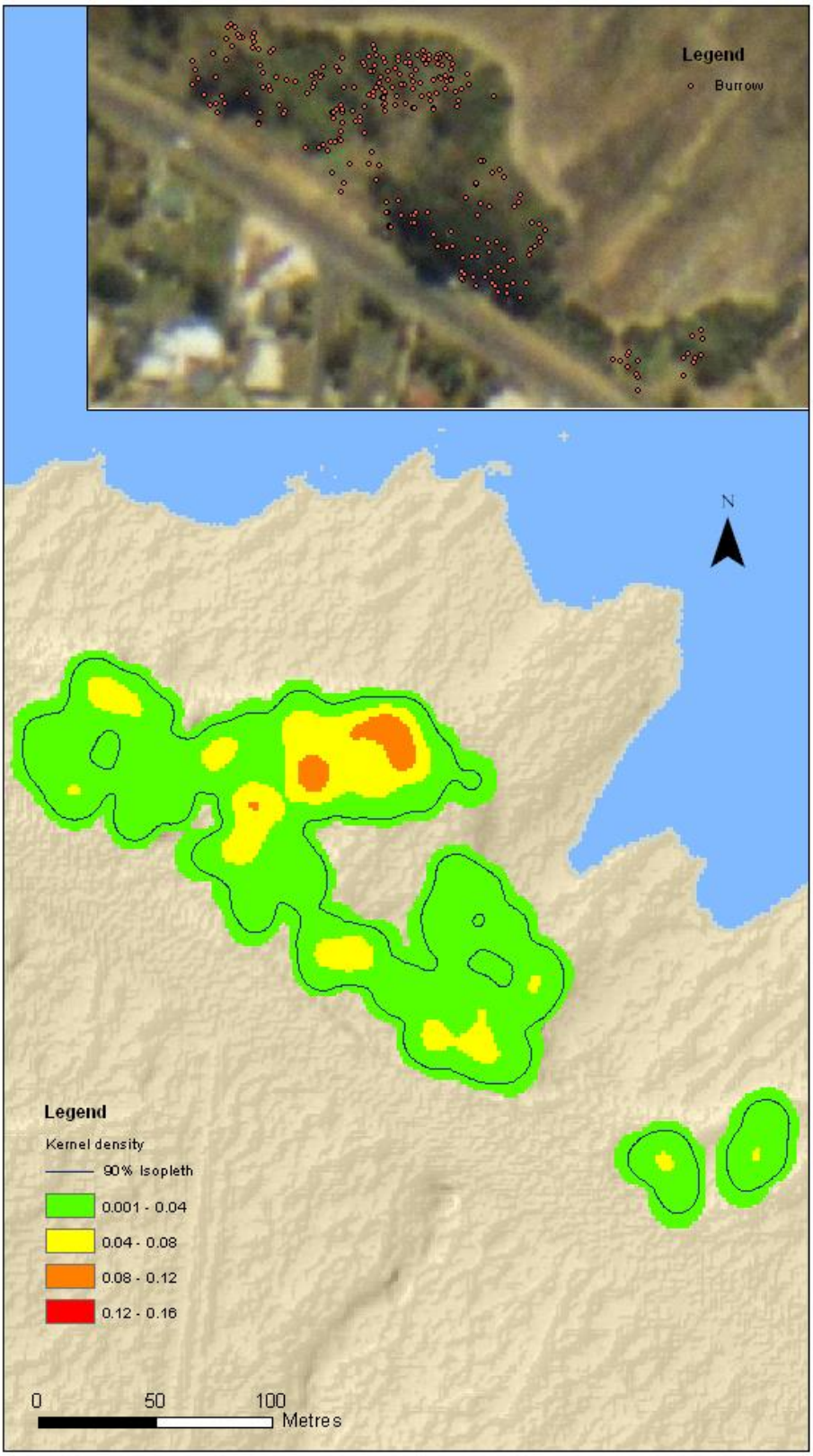


Figure 2-9 *Sulphur Creek little penguin colony. Kernel density plot with a higher density illustrated in orange in three patches in the sampled area. The inset shows the burrow locations.*

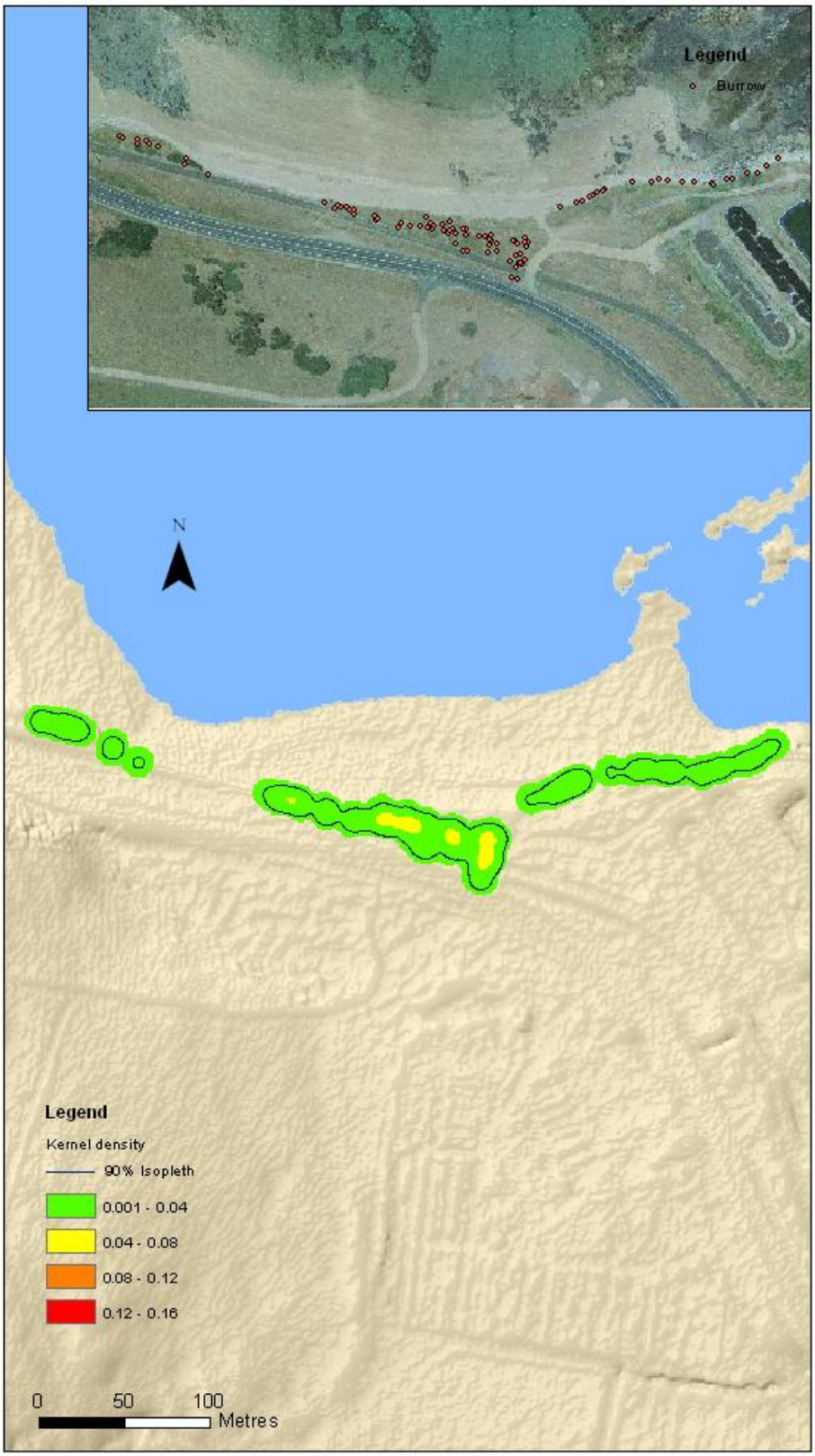


Figure 2-10 *Woody Point little penguin colony. Kernel density plot with absence of the higher density values present in other colonies. The majority of the burrows are grass. The inset shows the burrow locations.*

Table 2-6 *Average Nearest Neighbour (ANN) ratio of burrow distributions in each colony. The negative values of the Z score indicate clustering of burrows whilst positive numbers indicate the dispersed pattern of the burrows. Larger negative or positive Z numbers indicate the more clustered or dispersedthe burrows are in the colony.*

Average Nearest Neighbour (ANN)	**Doctor's Rocks**	**Woody Point**	**Cooee Point**	**Ocean Vista**	**Parsonage Point**	**Sulphur Creek**
Observed Mean Distance:	2.66	3.19	3.78	4.19	2.43	2.58
Expected Mean Distance	3.92	2.76	3.95	3.49	3.44	3.67
Average Nearest Neighbour Ratio:	0.68	1.15	0.96	1.2	0.71	0.71
Z-score	-16.58	2.84	-0.85	4.5	-10.25	-9.33
p-value	<0.001	0.004	0.4	<0.001	<0.001	<0.001
Pattern	**Clustered**	**Dispersed**	**Random**	**Dispersed**	**Clustered**	**Clustered**

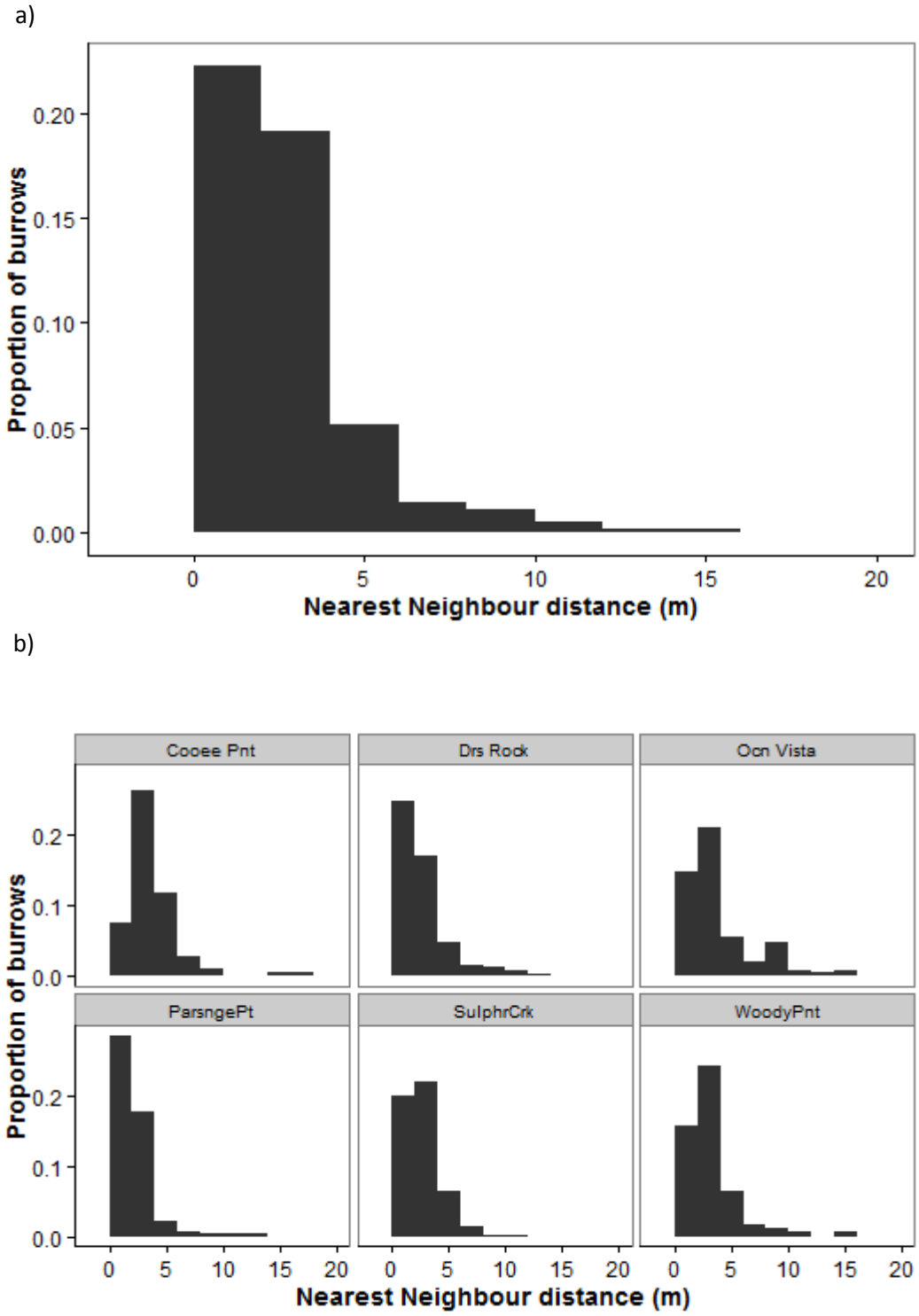


Figure 2-11 *Frequency plots of: a) Nearest Neighbour (NN) for all six study colonies. The majority of nests and burrows are within 5 m of each other across all colonies. b) NN results for each colony, showing that some variation exists among colonies, but general burrows are within 5m of each other large number of artificial burrows in Parsonage Point may account for the 2m nearest neighbour distance.*

2.4.4.3 Relationship between Nearest Neighbour distances and Burrow Type

Further investigation of the contributing factors to the clumping of burrows in the colonies found that Nearest Neighbour (NN) was significantly different among the different types of burrows (Figure 2-13). Analysis of variation of NN *versus* burrow type ($F_{(9,1659)} = 8.527$, $p < 0.0001$) indicates that the variation of NN among burrow types is highly significant. Post hoc Tukey HSD testing (Table 2-7) indicated that vine burrow types were more closely spaced compared to the other burrow types (Table 2-7).

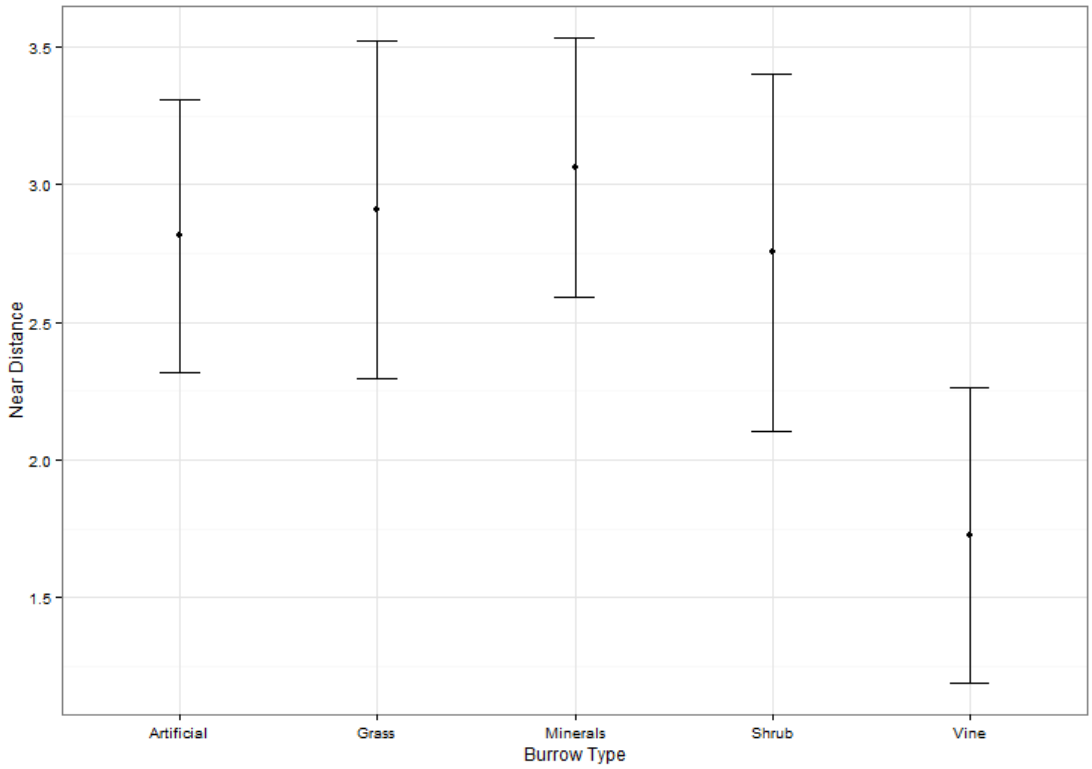


Figure 2-12 *Plot of nearest neighbour (NN) distance grouped by burrow type across all little penguin colonies. Nests in vines show the shortest distance between burrows overall and the smallest variation within the group.*

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Table 2-7 *Results of a post hoc Tukey HSD test showing adjusted p-values, showing the nearest negihbour distances among burrow types. The results indicate that the nearest neighbour distance among vine nest-sites differ significantly (bold) from most other little penguin burrow types.*

	Artificial	**Grass**	**Minerals**	**Shrub**
Artificial				
Grass	0.5070050			
Minerals	0.9974664	0.8735210		
Shrub	0.9744100	0.9993508	0.9998686	
Vine	**0.0000004**	**0.0000000**	**0.0000000**	**0.0000014**

2.4.4.4 Relationship of width of colonies to cluster

The distance of each burrow to each side of the colony perimeter was measured and the sum of the two distances gave the width of the colony at each burrow point. The relationship between the NN and the width of each colony was not significant as a contributing factor to the clustering of the colonies (ANOVA $F_{(1, 1663)} = 3.046$ $p > 0.05$).

2.5 Discussion

The spatial scale at which patterns are investigated can provide ecological insights into a species and how it utilises the available habitat. At the geographical, Tasmania-wide, 100 km *meso*-scale, penguin colonies around the coastline were dispersed. This suggests that little penguins use colonies based on some characteristic of the location, rather than a random distribution. The three main reasons suggested to explain why seabirds form colonies in an area are 1) to be close to foraging areas, 2) to minimise the effect of predators and 3) to socialise and interact (Furness & Monaghan 1987). However, what determines exactly where colonies form probably includes other factors such as suitability of terrestrial habitat, which would be influenced by the local topography.

Larger and more densely packed colonies compared to small and elongate colonies would be expected to offer more protection from predators. Most of the colonies have formed along the coast in an elongate shape, as indicated by the Perimeter/Area ratio (Table 2- 5). On the mainland of Tasmania only one very large colony at Point Sorell exists that has minimal anthropogenic pressure, and low presence of introduced vertebrate predators. The remaining large little penguin colonies that are less threatened by introduced vertebrates are found on islands in the Bass Strait.

The pattern of colony locations around the North West Coast indicates a dispersed distribution, but this could be due to where the boundaries of the study area were placed on the map for the ANN. If the area had been extended to include other colonies to the east of the Devonport boundary, then the ANN may have indicated a clustered distribution. The extent of the regional area studied clearly needs to be taken into account in the interpretation of the results of spatial analysis. In particular the use of ANN analysis requires a more defined geographic boundary. Anecdotal information suggests that larger colonies along the North West Coast have been present for at least 50 years. Some smaller colonies (e.g. Fossil Bluff, Wynyard) have disappeared due to predation by domestic dogs in the 1990s. Dogs have also affected other colonies along the coast and some have decreased in number (P.Marker pers. observ.). Local knowledge suggested the existence of other colonies in the past along the coast that have now also disappeared (e.g. at Rocky Cape). All the colonies that have been identified (Figure 2- 2) have been present since the 1990s and in some areas locals report that the size of the nesting area has increased.

2.5.1 Regional scale

This study has identified 17 colonies that are regularly distributed along the North West Coast of Tasmania. However, analyses at *meso* scales (10 - 100 km) may suggest that there is only one colony when examining a map. Hence the 17 colonies could be remnants of one or more larger colonies that have been fragmented into a pseudo-regular pattern as a result of coastal development. If a scale of spatial independence is taken into account (Table 2-4) then may be that many of these colonies are actually sub-colonies or fragments of a larger colony in the area. Such fragmentation may be due to the changing habitat quality of the area, the limited coastal habitat available and the constraints placed on the expansion of the colonies inland. The role of human activities in the fragmentation of available habitat is unknown but cannot be ignored. It is speculated here that perhaps there could be a spatial scale of independence of colonies whereby a distance of greater than > 2 km would indicate a distinct, separate colony. Consequently there may only be 8 colonies in the area. However, as the spatial scale of demographic independence is unknown, the number of colonies in this area could vary from 8 - 17 (Table 2-4).

Foraging areas of little penguins along this coast are unknown, but based on studies of little penguins at Phillip Island, Victoria, it would seem that foraging trips are within 30 km of colonies during the breeding season (Collins *et al.* 1999; Hoskins *et al.* 2008). This would imply that most of the little penguins forage in overlapping areas of the coast due to the proximity of the colonies. Thus, competition for food among colonies is an unlikely explanation for the dispersed pattern of colony distribution.

The concept of a metapopulation of little penguins has been demonstrated for Southeast Australia (Overeem *et al.* 2008; Peucker *et al.* 2009). Phylogeographic analysis for Southeast Australia over a distance of 860 km shows genetic homogeneity (whereby the exchange of only one gene per generation defines homogeneity) amongst little penguin colonies. So it is quite possible that the fragmentation of the habitat along the North West Coast (Figure 2-3) has resulted in patches of habitat where many small colonies of penguins are found rather than fewer larger colonies.

The scale of demographic independence is hard to define (Table 2-4) but it is likely that the close proximity of these colonies would support the hypothesis of a high degree of genetic similarity, or at least some gene flow, by just the smallest number of movements of birds amongst colonies, though this warrants further investigation. Population connectivity is often measured by genetic analysis as it can be more difficult to measure dispersal between and among colonies (Lowe & Allendorf 2010). Pedigree analysis at the individual level would ascertain the closeness of the relationship among the penguins in these small colonies across the North West Coast. However, a combination of genetic studies and demographic capture / mark / recapture studies would provide a more complete picture of the ecological connectedness among the colonies as the two aspects provide complementary information (Lowe & Allendorf 2010).

Dispersal of little penguins is infrequent, especially in Southeast Australia as penguins are highly philopatric (Dann *et al.* 1992a; Priddel *et al.* 2008; Peucker *et al.* 2009),. But movements between colonies or patches in a landscape could imply that within the sampled area the apparent colonies are patches of a much larger colony. It has also been suggested that a landscape could have a metapopulation capacity which would support a species to a certain extent (Hanski & Ovaskainen 2000).

2.5.2 Colony scale (*Topo* scale)

The average density of burrows ranged between 0.01 – 0.02 m^{-2} amongst the six study colonies, and appears to be within the same range as at Phillip Island and Notch Island. However, the density of burrows is a little higher than that measured on Wedge Island and other Tasmanian Islands (Table 2-8). Lower densities may be a consequence of the presence of other birds inhabiting the island, i.e. competition with short tailed shearwaters *(Puffinus tenuirostris*) which also inhabit these islands (Schumann, Dann & Arnould 2013), or simply that there is enough habitat to allow a wider spread of burrows , or that the populations have not reached carrying capacity. The proximity and availability of prey may also contribute to burrow density (Dann & Norman 2006).

Table 2-8 *Comparison of density of little penguin burrows in locations in Tasmania and Victoria*

Colony	**Density Burrows m^{-2}**	**Reference**
Doctor's Rocks – Sulphur Creek (see Table 2-4)	0.01 – 0.02 (5 colonies)	
Wedge Island (Tasmania)	0.002	(Vertigan 2010)
Phillip Island (Victoria)	0.012	(Sutherland & Dann 2013)
Rabbit Island (Victoria)	0.002	(Schumann, Dann, Hoskins, *et al.* 2013)
Kanowana Island (Victoria)	0.002	"
Notch Island (Victoria)	0.010	"
Cliffy Island (Victoria)	0.002	"

At the colony level, clustering of burrows occurs in three of the six study colonies, at least where there appears to be sufficient width for the colony structure to develop. For instance, at Sulphur Creek, where the colony width extends to 87 m, there is space for penguins to build burrows close to other depending on the nature of the material. However, lack of a significant relationship between the perimeter / area ratio of the colony and clustering would suggest that clustering is not related to the amount of habitat available, but more affected by the shape and the nature of the colony terrain (Chapter 3).

Whether clustering of nest-sites is a social behavioural response by penguins, or a response to some favourable aspect of the habitat is difficult to differentiate. In some colonies, for example at Ocean Vista, nest-sites are dispersed to some degree, and whilst this may be an effect of antagonism or interference between penguins, it may also reflect a lack of habitat to allow clustering to take place. Nest-sites within a colony can also demonstrate more than one level of structuring, with clustering being demonstrated by some nest-sites but then a regular distribution within those clusters. However, if this was the case, then it would be seen at the colony scale too. In some colonies there are a few burrows with a NN distance of greater than 5 m. This could be where patches of the landscape are being used as a "last resort" when the better sites are already occupied. It may also simply mean that in the year of observation other nest-sites were unused and hence were not accounted for in the study. Nest-sites placed at a greater distance from other nests could imply that the chances of mating are reduced as the frequency of visitation of birds to the burrow is reduced. A longer term study which monitors the sequential use of nest-sites over a number of years would provide insights into their frequency of use and might indicate which types of nest-site s are more favoured by little penguins.

2.5.3 Intra colony distribution related to the type of burrow

The kernel density indicates that there are only a small number of patches that contain a relatively high nest density and that they occur in the three colonies identified as including clusters. Analysis of the NN results suggests that vines, in particular native species such as bower spinach (*Tetragonia implexicoma*,) and introduced vines such as cape ivy *(Delirea odorata)*, honeysuckle (*Lonicera periclymenum)*, and rambling dock (*Acetosa sagittata)*, tend to be associated with burrow clusters. Whenever these plant species are present, the density of burrows is higher than in other combinations of burrow types. In many cases, vine species tend to grow over other vegetation, trees and logs, providing burrows that can be more densely spaced together. The burrows are well hidden, and the close proximity of the burrows to each other would increase the probability of males visiting other females in nearby burrows. A similar finding was noted in yellow-eyed penguins (*Megadyptes antipodes*) where nests were also observed to be in greater density under thicker vegetation and decreased as the vegetation thinned (Seddon & Davis 1989). Greater protection from predators in the more densely clustered regions of the colony could also occur, but this may lead to increased parasite infestation due to closer proximity of the nests (Duffy & Deduffy 1986). The extra nutrients provided by penguin faeces could assist the growth of the vines (Kazama *et al.* 2013) and this may be a factor contributing to the dense nature of the vegetation and subsequent nest-sites.

Generally nests in the centre of a colony provide more protection from predators, as proposed by the central periphery hypothesis (Wittenberger & Hunt Jr 1985; Siegel-Causey & Kharitonov 1990) and the "selfish herd" effect where an individual's survival is determined by the number of neighbours present (Hamilton 1971). The central periphery distribution hypothesis was tested on a colony of black legged kittiwakes (*R. tridactyla*) (Coulson 1968) and also on other seabirds (Furness & Monaghan 1987; Kharitonov & Siegel-Causey 1988). The studies found that birds in the central area had a higher breeding success than that of birds breeding on the periphery. However, studies of other seabird species have not supported this hypothesis; no difference in breeding success was found between the centre and edge of the colonies of two European shag (*Phalacrocorax aristotelis*) colonies in the western Palaearctic (Velando & Freire 2001) and ring billed gulls (*Larus delawarensis*) (Ryder & Ryder 1981). It could be argued that surface nesters are generally easily seen so that predators are more likely to attack at the periphery of a colony, or a flying predator may be successful in attacking its prey anywhere in the colony. Burrowing seabirds are generally not visible during the day and any location may be equally subject to predation, depending on the ease of access to the burrow by the predator.

If indeed there are not as many colonies through the overall study area as first hypothesised, and as individual colonies are elongate along the coast, then the notion of a "safe"

central part of the colony may not actually exist given the short distances between the peripheries and the centres of elongate colonies. There may in fact be a central colony that exists along the coast, but this would need further investigation as other colonies identified (Figure 2-3) would need to be more carefully surveyed.

2.5.4 Implications for conservation and management

In a review of little penguins in Victoria, it was suggested that breeding colonies are constrained by the availability of burrowing sites, particularly on smaller islands (Dann & Norman 2006). It is highly likely that the unique habitat constraints posed by human impacts along the coastline of the study area have caused the expansion of penguins along the shore instead of in an inland direction. Overall, colonies along the North West Coast of Tasmania are still viable despite the peri-urban nature of their distribution. However, they have experienced increasing pressures such as loss of habitat due to coastal development and consequently an increased presence of people traversing across colonies to access beaches. Coastal erosion has also resulted in habitat loss in some of the coastal colonies due to stronger storm surges that occur during winter (P.Marker pers. obs.). Resulting steeper slopes of sand dunes has more than likely increased difficulty in accessing habitat. This is known as "coastal zone narrowing" (Jackson & McIlvenny 2011; Pontee 2013) and is predicted to increase in severity in the future. Local records also show that at least 180 birds were killed by dogs over the last eight years along the North West Coast. These records are not complete as they are only reported incidences rather than a planned and regular monitoring effort.

While just 3.5% of all bird species are seabirds, they are the most rapidly decreasing group of birds globally (Croxall *et al.* 2012). Threats are wide ranging and include at-sea risks as well as those at breeding sites, which are both extensively reviewed in Croxall et al. (2012). Seabird restoration programs have been used to expand existing colonies, restore populations and minimise threats (Jones & Kress 2012). Habitat rehabilitation has been used in many areas of the world's urban seabird colonies, which are under enormous pressure and require management to maintain them as viable breeding colonies. One aspect of conservation and management that may need consideration is the spatial pattern of colonies and the distribution of the burrows or nest-sites within them.

In this study, the distributional pattern of nest-sites and colonies at the state-wide and regional scales were analysed, and whilst clustering was observed in some colonies at the nest-site scale, two colonies showed dispersion of the burrows. The multiple levels of spatial scale or levels of organisation may require a different management approach (Hobbs 1998). Community groups are often involved in caring for their "local patch" and in many instances have been

successful at careful planting of appropriate vegetation. In fragmented colonies such as those that exist in this study, it would seem that increasing the density of available burrow sites might be a possible solution to resolving the lack of habitat. It may even be possible to place artificial burrows in dense patches to simulate clustering, especially where there is an absence of dense vegetation cover, such as vines. Another possibility would be to increase the vegetation cover density and promote vine cover.

The spatial scale should also be taken into account in conservation and management decisions, to account for the variation at the landscape level at which a species operates. Resources both human and financial are limited, requiring strategic planning to maximise the conservation of a species and its habitat. This study suggests the possibility that improving vegetation cover or increasing clustering of burrows may be useful tools in conservation management for little penguins and one method to improve some of the marginal habitat in peri-urban areas where habitat availability is diminishing or is closed off to from penguins.

CHAPTER 3

Modelling the characteristics of nest-sites of a burrowing seabird, the little penguin (*Eudyptula minor)*

3 Modelling the characteristics of nest-sites of a burrowing seabird, the little penguin (*Eudyptula minor)*

3.1 Abstract

As all seabirds must breed on land, habitat during the breeding season is important. Nest-sites are either in the open, under vegetation or underground. This study developed a model of nest-site habitat for little penguins using the terrain variables: *slope, elevation, aspect, solar radiation* and *wetness index* as well as *distance to the coast* for each burrow derived from a digital elevation model (DEM). Accurate positions of burrows were determined in six colonies using differential GPS and the aforementioned variables were derived at each point. Random points were generated from the DEM to represent locations where no burrows were found and the two datasets were then combined. The model indicated that burrows were generally found on shallow slopes in relatively warm and dry areas that received high levels of solar radiation. The model explained 62% of the variation for predicting the presence of burrows but only 42% for predicting their absence. Thus unused habitat might have the capacity to support more nesting sites given suitable environmental conditions. This study is an example of how terrain variables obtained from a high resolution DEM can support model development by providing data that are not easily accessed in the field. Such a model can assist conservation and planning of suitable habitat for a species.

3.2 Introduction

The benefits of colonial breeding are expected to outweigh the costs of travelling to distant foraging areas (Block & Brennan 1993; Danchin *et al.* 1998). Many seabird species raise their offspring in colonies. Locations of these colonies are determined by proximity to foraging grounds. (Clode 1993; Ainley *et al.* 2004; Byrd *et al.* 2005; Ballance *et al.* 2009). Colonial seabirds use either surface or burrow nests, but in both cases the space required may result in competition with conspecifics (Bried & Jouventin 2002). Most seabirds are also highly philopatric to their native colony, though not necessarily to the same locality within the colony. Consequently, nest-sites are an important space for the breeding success of seabirds. The characteristics that determine their location within a colony have been the subject of many studies (Birkhead 1977; Olivier & Wotherspoon 2006; Schumann, Dann & Arnould 2013), but within a colony individual birds must make decisions about the exact positioning of their nest.

Nest-site locations within seabird colonies are determined by a hierarchical set of social, behavioural and habitat responses which are species specific (Brown & Brown 2002; Doligez & Boulinier 2008). The nests of seabirds that use an open surface tend to be regularly spaced, which may be more a territorial response than a habitat requirement. Conversely, the nests of seabirds that are under vegetation or in burrows are not only smaller, but also tend to be

either clustered or dispersed within the colony, which may be more a response to habitat characteristics than territoriality. Burrows offer climatic protection for chicks whilst parents are at sea foraging (Frost *et al.* 1976; Schramm 1986).

The choice of a nest-site within a colony can be based on proximity to mates and communication with other birds, as well as protection from predators (Schramm 1986; Brown & Brown 1987), but the fundamental aim is to produce chicks. Chick production determines how good the quality of the habitat is for breeding. Understanding the location of nests within colonies and the environmental variables that are associated with them has been the subject of much research on a variety of species. Several factors have been used in models that seek to explain nest-site location of many seabird species (Lawton *et al.* 2006; Urios & Martinez-Abrain 2006; Kassara *et al.* 2012). As little penguins nest underground or on the surface, it would be expected that there would be a preference for dry, warm burrows which are reflected in appropriate terrain variables, but they may also be influenced by physical characteristics of the habitat.

Abiotic (temperature, precipitation and topography) and biotic (species abundance, density and competition for resources) factors have been used in modelling studies to predict species distribution at landscape, regional and global scales (Guisan & Zimmermann 2000; Peters *et al.* 2004; Franklin 2009). Various theories have been developed to explain and predict the distribution of species using environmental variables and are discussed by Franklin (2009) and references therein. Two approaches of relevance are ecological niche models, which relate environmental variables to the fitness of a species, and habitat suitability models, which relate environmental variables to the likelihood of the occurrence of the species (Hirzel & Le Lay 2008). In the literature the term species distribution modelling is used interchangeably with habitat suitability modelling. These approaches to understanding the distribution of species have seen an enormous growth in recent literature and have become very useful for conservation and planning (Franklin 2009).

The choice of appropriate environmental variables is important to the development of a model and its application. However, no one set of environmental predictors is suitable for all species, so understanding which are the most appropriate for a particular species is a critical step in the development of habitat suitability models (Austin 2002; Ashcroft *et al.* 2011; Williams *et al.* 2012). Topography produces indirect gradients which then influence direct gradients of soil type, precipitation, temperature and incident solar radiation (Guisan & Zimmermann 2000). These in turn influence vegetation type and the presence or absence of other biota. Topographic variables can be easier to derive than direct variables, particularly if fine-scale digital elevation data are available. Consequently, Digital elevation models (DEM) at an appropriate scale can provide data that can be used in models as a much simpler alternative to having to collect data from the field.

The results of habitat modelling analyses may be strongly influenced by *grain* (resolution) and *extent* (size of the study area) (Turner *et al.* 1989), which are both associated with scale (Wiens 2002). To be useful, the resolution of the input data should match closely with the resolution of the response variable (Elith & Leathwick 2009). In this study, however, the same resolution is used for a combination of terrain factors: *elevation, slope, aspect, solar radiation* and *wetness index,* and the response variable (sample point) in a habitat suitability model. These variables have been selected as they reflect gradients that determine the impact of climate and soil factors on vegetation and the specific location used by burrowing seabirds.

In this chapter a habitat suitability model is developed, using terrain variables, to examine whether little penguins respond to characteristics in the landscape in their choice of nesting site, as this is expected to provide some measure of the capacity of the landscape to support nests. The model is based on terrain variables that can be extracted from a DEM, and that can explain the presence and absence of nest-sites.

The study area is based on the North West Coast of Tasmania where 17 colonies of little penguins have been identified along a 50-km stretch of coast. Little penguins tend to nest under vegetation or in burrows and these are generally clustered in their distribution within a colony (Chapter 2).

3.3 Methods

3.3.1 Data Collection

3.3.1.1 Location of colonies

Six colonies from the study area that represented a range of vegetation types were selected: Cooee Point (-41.00ºS 145.87ºE), Doctor's Rocks (-41.00ºS 145.77ºE), Ocean Vista (-41.03ºS 145.86ºE), Parsonage Point (-41.04 ºS 145.89 ºE**)**, Sulphur Creek (-41.00ºS 146.02ºE) and Woody Point (-41.03ºS 145.80ºE) (Figure 3-1). These areas were selected to provide a range of habitat types, based on vegetation. A colony was defined here as being a contiguous patch where burrows are located within 5 m of each other. Fieldwork was undertaken during the breeding seasons from December – March in 2008/2009, 2009/2010 and 2010/2011 when the presence of birds in the colonies was at its peak. A breeding season was defined as when birds start laying and incubating eggs, and raising chicks. The peak activity occurs during December to January.

Figure 3-1 *Locations of study colonies little penguins (Eudyptula minor) in NorthWest coast, Tasmania*.

Output accuracy is only as good as input data and tools used in the process. The use of DGPS provides better accuracy and precision in recording the placement of a location (such as a nest-site) in the landscape than a handheld GPS, or earlier approaches such as mapping points onto an arbitrary grid. The horizontal accuracy of the DGPS used is 20 cm which is better than the 5-10 m obtained from most handheld GPS. The DGPS is also more reliable as it less prone to outliers. This reliability was obtained by use of a local base station and transmission to a rover in real time which improved the user position (Appendix 1). Also, using a 1 m DEM means that the pixel sizes (1 m x 1 m) produces better height quality than lower resolution 5 m DEM. Consequently had GPS data been combined with 1 m DEM points, they may have been placed up to 5m away resulting in a different height, depending on the terrain. It is expected that using a lower quality GPS (i.e. handheld GPS) would have produced lower quality results.

Real-Time Kinematic (RTK) surveying using Global Navigation Satellite Systems technology (GNSS) was used to map the nest-site locations as this provides at least 20 cm accuracy. The ProMark 3 single-frequency RTK Differential GPS (DGPS) system used two GNSS antennae, with one a static point at a known location referred to as the base station (Figure 2-1a) and the other attached to a backpack on the recorder known as the rover (Figure 2-1b). Single-frequency RTK mapping is a relative positioning technique which measures the position of the two antennae relative to each other in real time.

The following protocol was used:

1 The base station which was in close proximity to each colony had a clear sky view. There were minimal surrounding obstructions and the transmitting radio antenna was positioned as high as possible. Once the base station had been collecting data over a known point for a minimum of 5 h, the data were transmitted as a Receiver Independent Exchange Format RINEX file to the Precise Point Positioning (PPP) online service operated by the Geodetic Survey Division of Natural Resources Canada called CSRS-PPP (http://webapp.geod.nrcan.gc.ca/geod/tools-outils/ppp.php) in order to obtain the position of the base station.

2 Locations of nest-sites were only recorded when there was a minimum of six satellites available. In 90% of cases a signal was received from nine or more satellites. All satellite signals were received from an angle of at least 10^0 above the horizon and the positional dilution of precision (PDOP) of > 99% of the readings was < 3. Positional dilution of precision values measure data quality in regards to the geometry of the satellites in view; a value of < 3 is considered excellent and indicates high precision. In 0.6% of the readings, the PDOP was between 4 and 5 (Table 3-1) which is still in the

"good" range. Locations were recorded every second and averaged over 20 s. All mapping of nest locations was conducted in UTM WGS84 Zone 55.

3 The rover data were downloaded via Mobile Mapper and converted to shape files for analysis in ArcGIS 10.

Table 3-1 *The mean and standard deviation (SD) of the positional dilution of precision (PDOP) of the colony locations recorded for little penguin nest-sites. All colonies show mean PDOP < 3, which indicates the readings are of very high quality. The high number of satellites also increases accuracy of GPS signals.*

Colony	Number of burrows	PDOP		Average number of satellites
		Mean	SD	
Cooee Point	107	1.66	0.31	10.13
Doctor's Rocks	727	1.77	0.35	9.92
Ocean Vista	137	1.48	0.31	10.91
Parsonage Point	335	1.66	0.26	10.30
Sulphur Creek	270	1.77	0.40	9.33
Woody Point	93	1.52	0.18	11.26

A nest-site was defined as a hollow in vegetation where penguins nest on the surface using vegetation as a cover, or a burrow where penguins dig under the soil surface or other substrate, such as rocks. Both were treated as a nest-site and were identified due to the presence of scats, feathers, tracks or smell. A very distinct fishy smell could be detected when chicks were present in the burrows. Only nest-sites that were currently being used by penguins were recorded.

To locate all the burrows in the sections of colonies being mapped, 3 people searched for the burrows in a systematic way. Nests were tagged with pink flagging tape. A second search was done to make sure no active nest-sites had been missed on the first pass. Nest-site locations were then logged using Promark 3 units. The recording of each burrow involved standing at the entrance and logging the point for a minimum of 20 s to ensure correct positioning. The attributes (burrow type, vegetation in a 1m quadrat in front of the burrow, substrate of each burrow, orientation of entrance) of each nest-site were concurrently recorded in a field book.

3.3.1.2 Burrow type

Burrow type was defined according to the material that formed the roof of the nest-site. For example, where nest-sites were dug into sand and had a sand roof, they were identified as a sand burrow, whereas a burrow with a sandy floor, but covered in vegetation was characterised by the specific type of the vegetation (Table 3-2). The vegetation was classified using the CSIRO handbook (Hnatiuk 2009) which records vegetation in a semi quantitative manner. It uses the National Vegetation Information System (NVIS) framework (ESCAVI 2003).

Table 3-2 *Classification system of vegetation structure used by little penguins showing examples for each category. See appendix 1 for a full list of vegetation species identified in the study sites.*

Classification categories of burrow types	Examples
Artificial	Black plastic pipe, concrete pipes or slabs, tyres, concrete igloos
Grass	Knobby Club Sedge *Ficinea nodosa*, Marram *Ammophila arenaria*, Onion weed *Asphodelus fistulosus*, Rush *Juncus* sp., Sagg *Lomandra longifolia*, Sedge *Carex* sp., Tussock grass.*Poa* sp.
Herb	Buzzy *Acaena* spp., Fire bush *Senecio prenanthoides*
Minerals	Rock, sand or soil
Shrub	African boxthorn *Lycium ferocissimum*, African daisy *Arcotis stoechadofolia*, Coastal boobyalla *Myoporum insulare*, Coastal saltbush *Rhagodia candolleana*, Coastal wattle *Acacia longifolia var. sophorae*, Correa *Correa alba*,
Tree	Pine *Pinus radiata*, Swamp paperbark *Melaleuca ericifolia*
Vine	Bower spinach *Tetragonia implexicoma*, Cape ivy *Delirea odorata*, Honeysuckle *Lonicera periclymenum*, Periwinkle *Vinca major*, Pigface *Carpobrotus* sp., Rambling dock *Acetosa sagittata*
Wood	Logs, Branches
Fern	Bracken *Pteridium esculentum*

3.3.1.3 Digital Elevation model

A digital elevation model (DEM) is a baseline data layer used in a GIS environment (Guisan & Zimmermann 2000), and is a raster representation of a continuous surface. The accuracy of the data is determined primarily by the resolution (distance between two points); the higher the resolution of the DEM, the more fine-scale features can be captured and used in analysis. The DEM used in this study was based on LiDAR (airborne laser scanning) point data produced for the ACE CRC Climate Futures project in 2008. The DEM has a 1 m x 1 m pixel resolution in the horizontal and vertical planes. It was supplied via the Information and Land Services Division (ILS) of the Department of Primary Industries, Parks, Water and Environment (DPIPWE). Data was captured in WGS84 and converted to GDA 94. All layers were projected in GDA94 MGA zone 55. The following derivatives were extracted from the DEM: elevation, slope, and aspect, and two calculated values: solar radiation and wetness index. Maps of each of the first three variables were derived for each colony to show their distribution.(Figures 3-2 – 3-7). The distance to the 1.83 m Highest Astronomical Tide (HAT) contour line (representing the

coast line) was also calculated for each burrow point. All DEM calculations and GIS processes were undertaken in ArcGIS 10.0 (ESRI 2011).

3.3.1.4 Terrain variables

Elevation

Height above sea level derived from the DEM.

Slope

The slope is a value of a plane calculated using the average of a 3 m x 3 m neighbourhood

$$\text{Slope}^{o} = \text{ATAN}\left(\sqrt{([dz/dx]^2 + [dz/dy]^2)}\right) * 57.29578$$

Aspect

The aspect was identified as the downslope direction of the maximum rate of change in value from each cell to its neighbours. Units were positive degrees from 0 to 359.9^{o} measured clockwise from the north and sine transformed. Flat surfaces were indicated by -1.

Solar radiation

Solar radiation was modelled, accounting for latitude, topography and atmospheric conditions between December - March, the period that the nest-sites were used. An upward-looking hemispherical view was calculated for each cell based on topography; a direct sun map and diffuse sky map were overlaid on this for each time interval (here, for every 60 min in five months) to calculate a composite insolation value in Wh/m^2.

Topographic Wetness Index (Windex)

Wetness index (*Windex*) is a function of the upstream area and the slope of the target cell and the measure is based on the relative position of a cell within the catchment. It is used as a proxy for variability in soil wetness and assumes a uniform substrate and ground cover (Beven & Kirkby 1979). The SAGA wetness index (SAGA: System for Automated Geoscientific Analyses. http://www.saga-gis.org/en/index.html) iterates the value so that an average is taken as follows:

$$Windex = \ln(A/\tan ß),$$

where A = upstream area and ß = Slope in degrees

Cells with lower values (close to 1) are dry cells whereas cells with higher values (closer to 20) are wet cells.

Distance to coast (DCst)

The distance to coast (*DCst*) was calculated using the Euclidean distance measured from a nest-site or random point to the highest astronomical tide (HAT) 1.83m, by the shortest distance between the sites / point to the HAT.

To develop the model, a set of locations representing absence of burrows was required and these were randomly generated from the DEM within each of the six colony boundaries. Equal sets of random points to burrow points were generated for each colony. The process outlined above was then used to extract *Elevation, Slope, Aspect, Solar radiation, Windex* and *DCst* for each of the randomly generated points.

3.3.2 Statistical analysis

3.3.2.1 Habitat suitability model

A generalised linear mixed effect model (GLMM) (Zuur *et al.* 2009) with a logit link and binomial response was used to determine the effect of the terrain variables *Elevation, Slope, Aspect, Solar Radiation, Wetness Index (Windex)* and *Distance to Coast* (*DCst*) on the occurrence of penguin burrows in each of the six colonies. The glmer function in package *lme4* version 1.0-4 in R was used (Bates *et al.* 2013; R Core team 2013). Colony (*Location)* was included as a random term in the model (Zuur *et al.* 2009). The variables *Slope*, *Elevation* and *DCst* were log - transformed and *Aspect* sine transformed to meet the assumptions of normality. After confirming a lack of collinearity between all transformed predictor variables (Pearson Correlation < 0.05), 32 models were run allowing for all possible combinations of variables as well as a null model that included no predictor variables. As all colonies had fences which restricted access to the coast the variable *DCst* was dropped from the model as its inclusion would have been biased.

The resulting 32 models were ranked and the fit evaluated using the Akaike Information Criterion (AIC) (Burnham & Anderson 2001); the most parsimonious GLMM having the lowest AIC value was considered the best. To test the reliability of the model, a new set of randomly generated points (extracted from the DEM) was added to the data set of burrow points. The GLMM process as described above was repeated a further nine times providing ten trials in total. Models were ranked and evaluated in each of the nine other trials using the AIC value to identify whether any one model consistently appeared.

To test the performance of the model selected, i.e. the model's ability to predict the occurrence of burrows accurately, a leave-one-out cross-validation process, based on removing

one point at random from the data, re-running the model on the remaining data and comparing the resulting predicted with the observed values was repeated 1000 times.

3.4 Results

3.4.1 Colony level – terrain variables

The six study colonies were located in peri-urban areas and their inland extent is constrained by infrastructure. The colonies were elongate and narrow with the width of habitat ranging from 4 m at Ocean Vista to 87 m in the Sulphur Creek. The Perimeter/Area (P/A) ratios varied between 0.2 at Ocean Vista to 0.05 at Sulphur Creek (Table 3-3). The more elongate and narrower colonies have higher values.

Figures 3-2 – 3-7 show maps illustrating the distribution of the nest-sites in each colony along with their elevation, slope and aspect derived from the DEM. All colonies were < 6 m in elevation apart from Doctor's Rocks which has a small headland where elevation was > 15 m. Slope in all colonies was < 5^{o} apart from sections of rock-faces which have slope > 20^{o}. Nest-sites at Cooee Point are either north or west facing, whereas in all other colonies are generally north or east facing. In a few instances some nest-sites e.g. at Woody Point are south facing.

Table 3-3 *Summary characteristics of the six study colonies of little penguins in North West coast, Tasmania.. Area and perimeter values calculated from the polygons of the study areas in GIS were used to calculate the Perimeter / Area ratio which provides a relative comparison of the shape of the colony. The more elongate and narrower colonies have higher values. For instance, Ocean Vista with a perimeter / area ratio of 0.2 is the narrowest and most elongate of the six colonies.*

Colony name	Lat Long	Description of colony	Study area in colony (m^2)	Perimeter to area ratio	Number of burrows	Estimated number of pairs of little penguins	Density Burrows/m^2
Cooee Point	-41.00ºS 145.87ºE	Old disused land with mostly artificial burrows added to supplement rock burrows. Patchy vegetation.	6663	0.13	107	94	0.02
Doctor's Rocks	-41.00ºS 145.77ºE	Coastal reserve area with a mixture of varying vegetation and burrow types	42733	0.06	727	664	0.02
Ocean Vista	-41.03ºS 145.86ºE	A very narrow strip of coastal vegetation with a mixture of varying vegetation and burrow types	9894	0.2	137	117	0.01
Parsonage Point	-41.04 ºS 145.89 ºE	Colony sited on reclaimed land previously used as building tip site. Coastal vegetation re-established and artificial burrows supplement the area.	17663	0.08	335	305	0.02
Sulphur Creek	-41.00ºS 146.02ºE	Colony sited on the coastal foreshore with dense cover of weeds.	14526	0.05	270	267	0.02
Woody Point	-41.03ºS 145.80ºE	A small patch of land sited near a sewage treatment plant with mixed vegetation.	7340	0.13	93	92	0.01

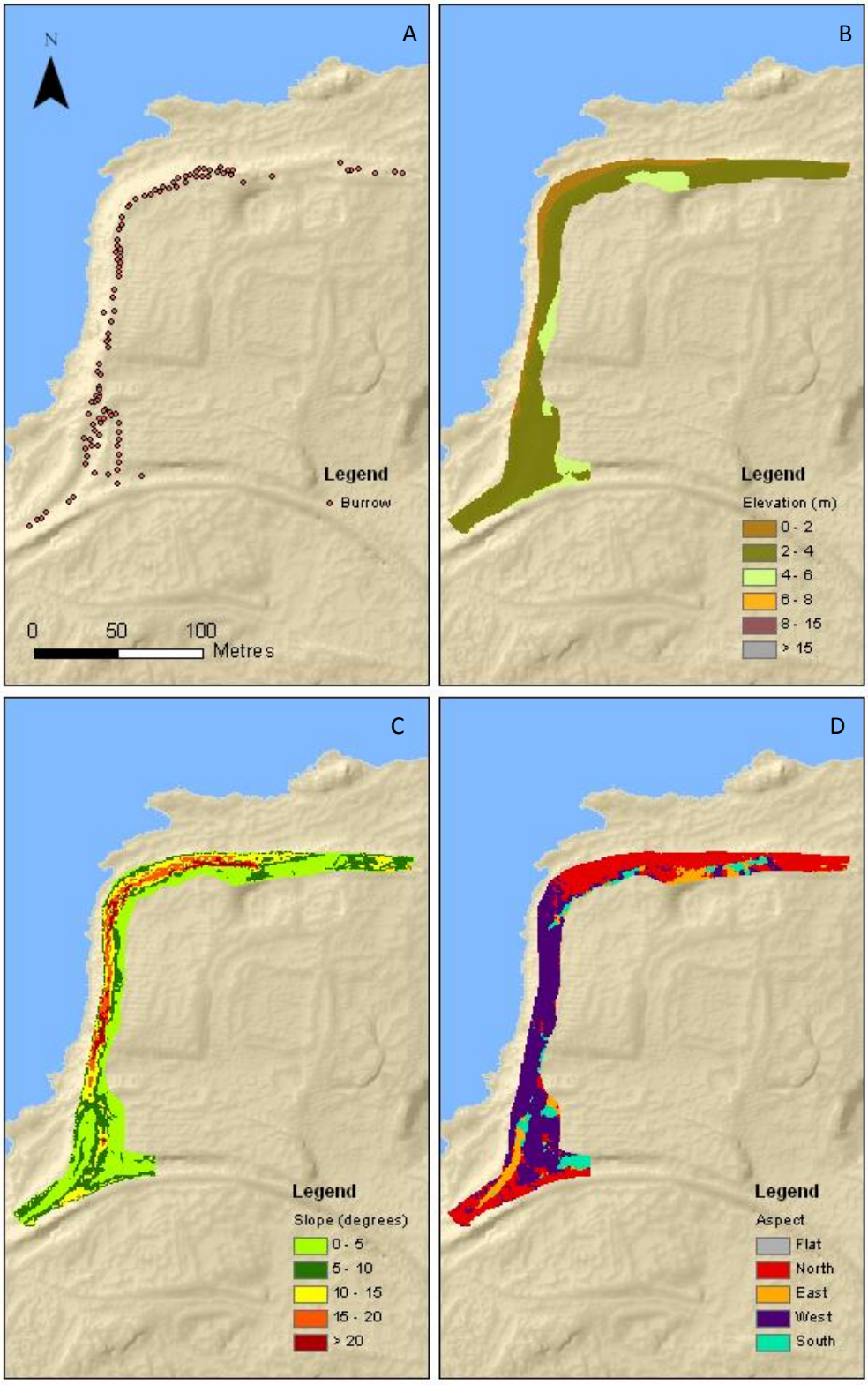


Figure 3-2 *Cooee Point A) Location of burrows, indicating a narrow linear colony. B) Elevation of colony; most is between 2-4 m. C) Slope – most is < 5°. D) Aspect – north and west facing terrain.*

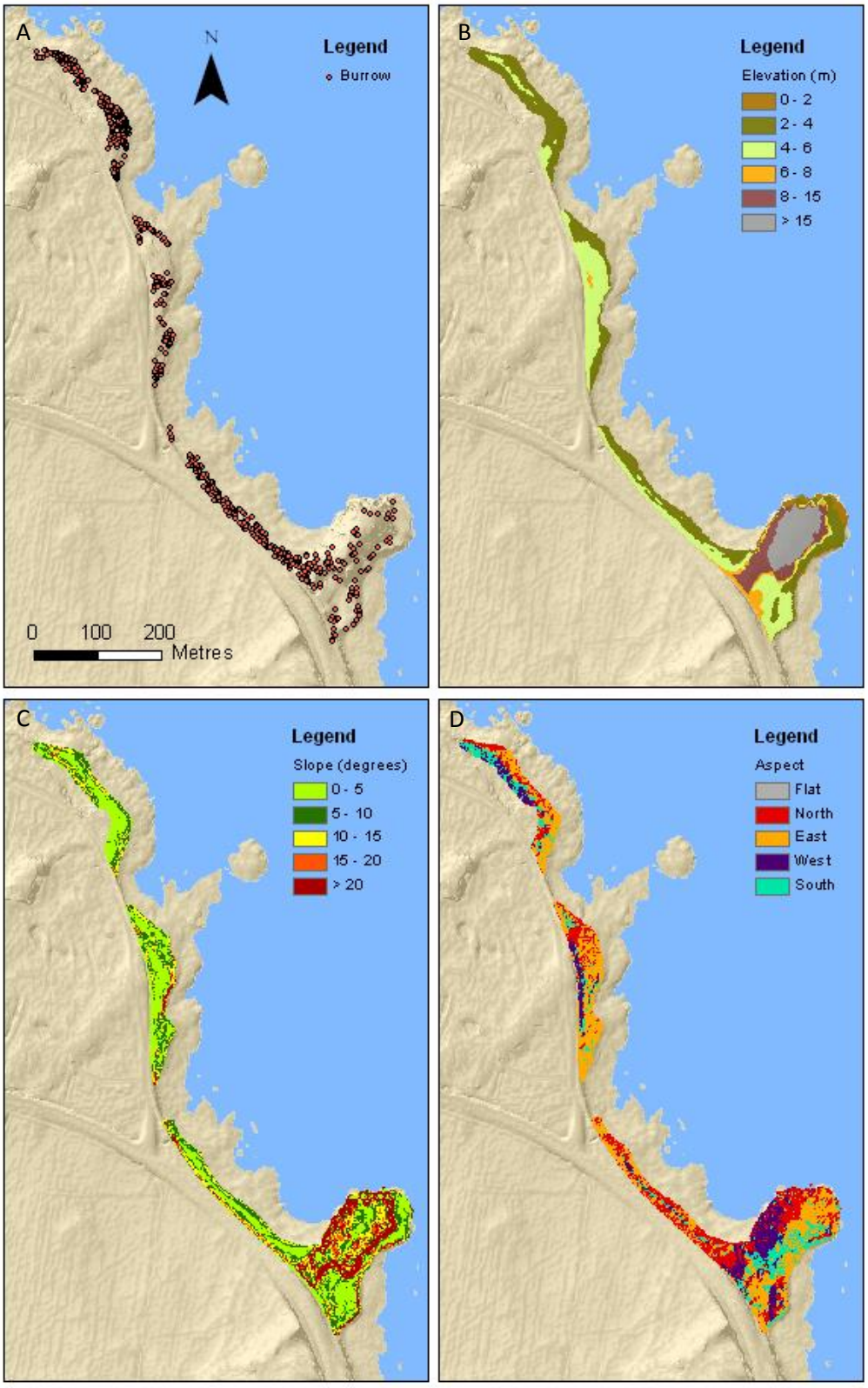


Figure 3-3 *Doctor's Rocks – A) Location of burrows, indicating a linear colony with a headland section at the bottom right. B) Elevation of colony, most of the terrain is <6m. C) Slope – most is flat between 0-5 degrees apart from the area around the headland. D) Aspect –north facing and east facing terrain.*

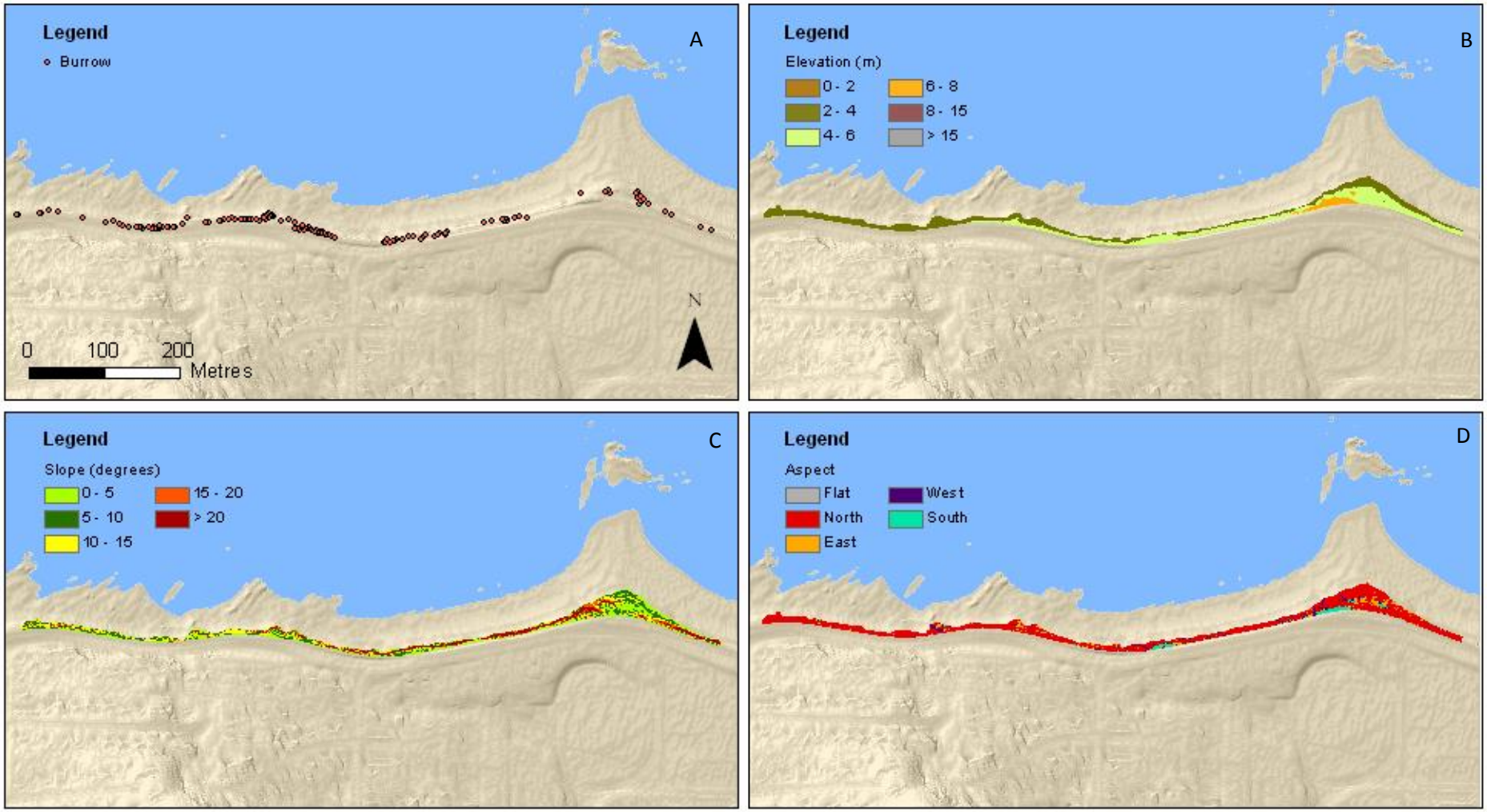


Figure 3-4 *Ocean Vista – A) Location of burrows is indicating a very narrow linear colony. B) Elevation of colony, most of the terrain is <6m. C) Slope – most varies 0-5 and 5-10 degrees. D) Aspect –north facing terrain.*

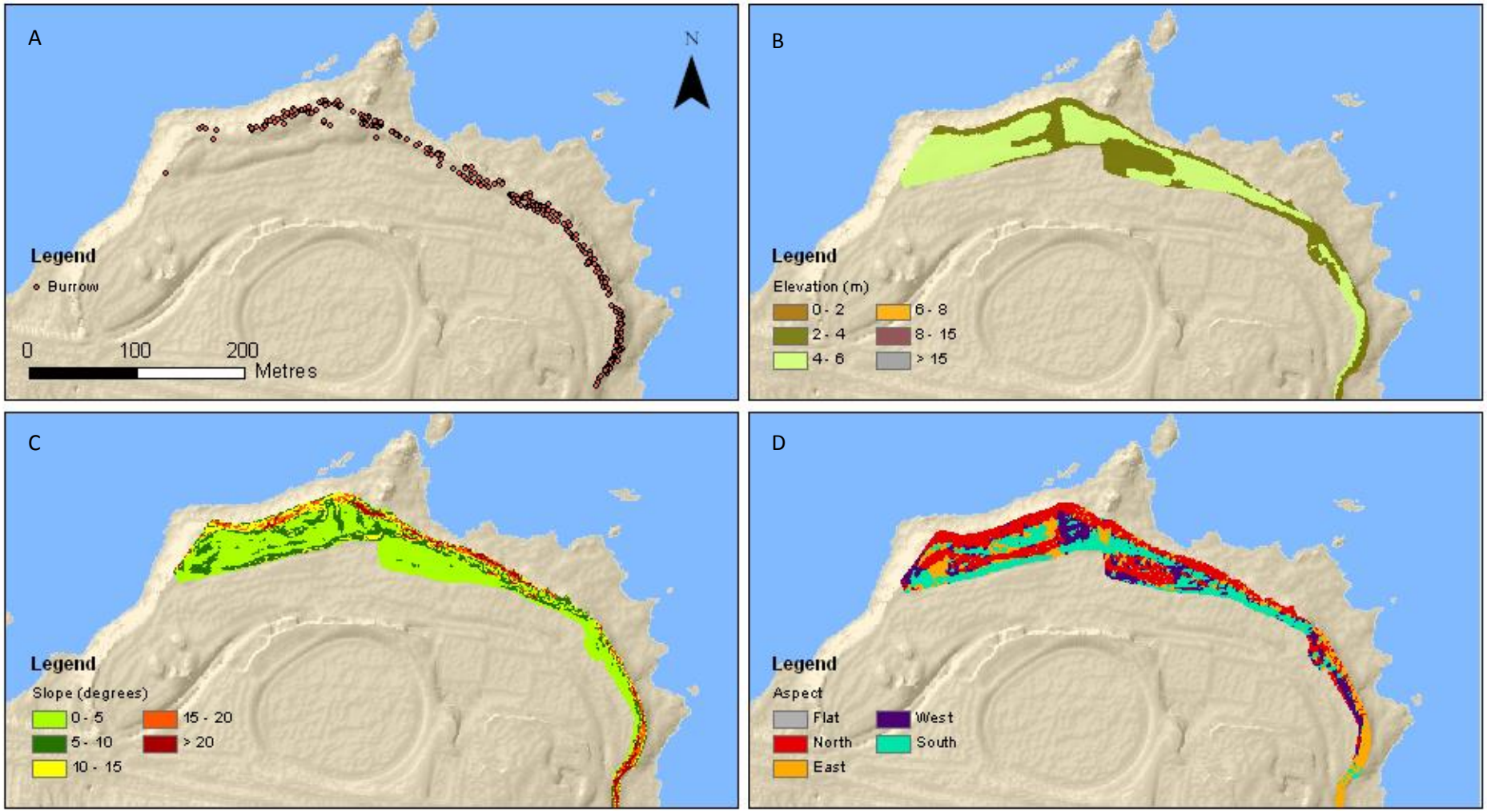


Figure 3-5 *Parsonage Point – A) Location of burrows, indicating a linear colony. B) Elevation of colony, most of the terrain is <6m. C) Slope – most 0-5 degrees. D) Aspect –north facing with some south facing terrain.*

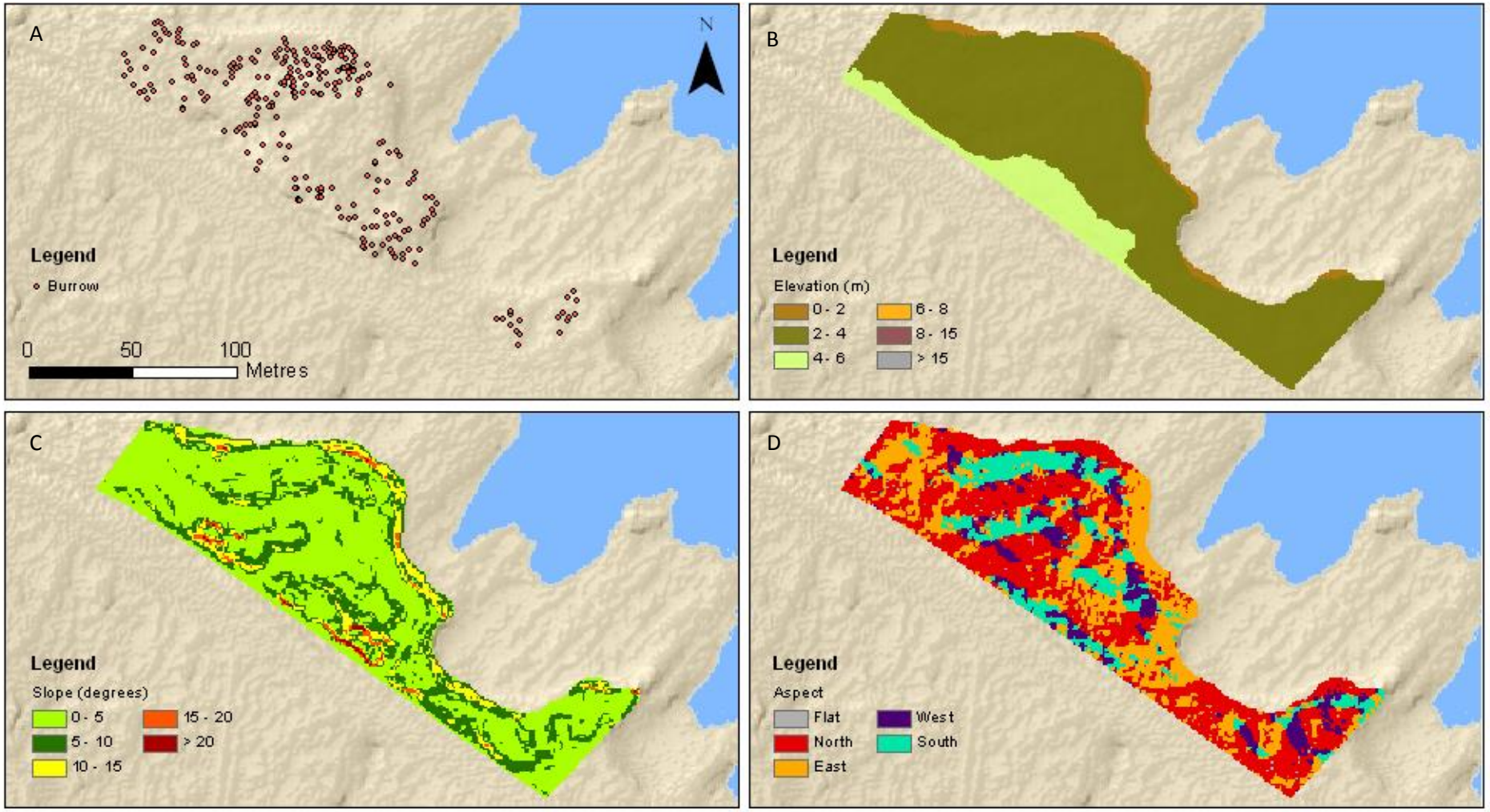


Figure 3-5 *Sulphur Creek – A) Location of burrows, indicating a rectangular shape. B) Elevation of colony, most of the terrain is <4m. C) Slope – most is 0-5 degrees. D) Aspect –north and east facing with some south facing terrain.*

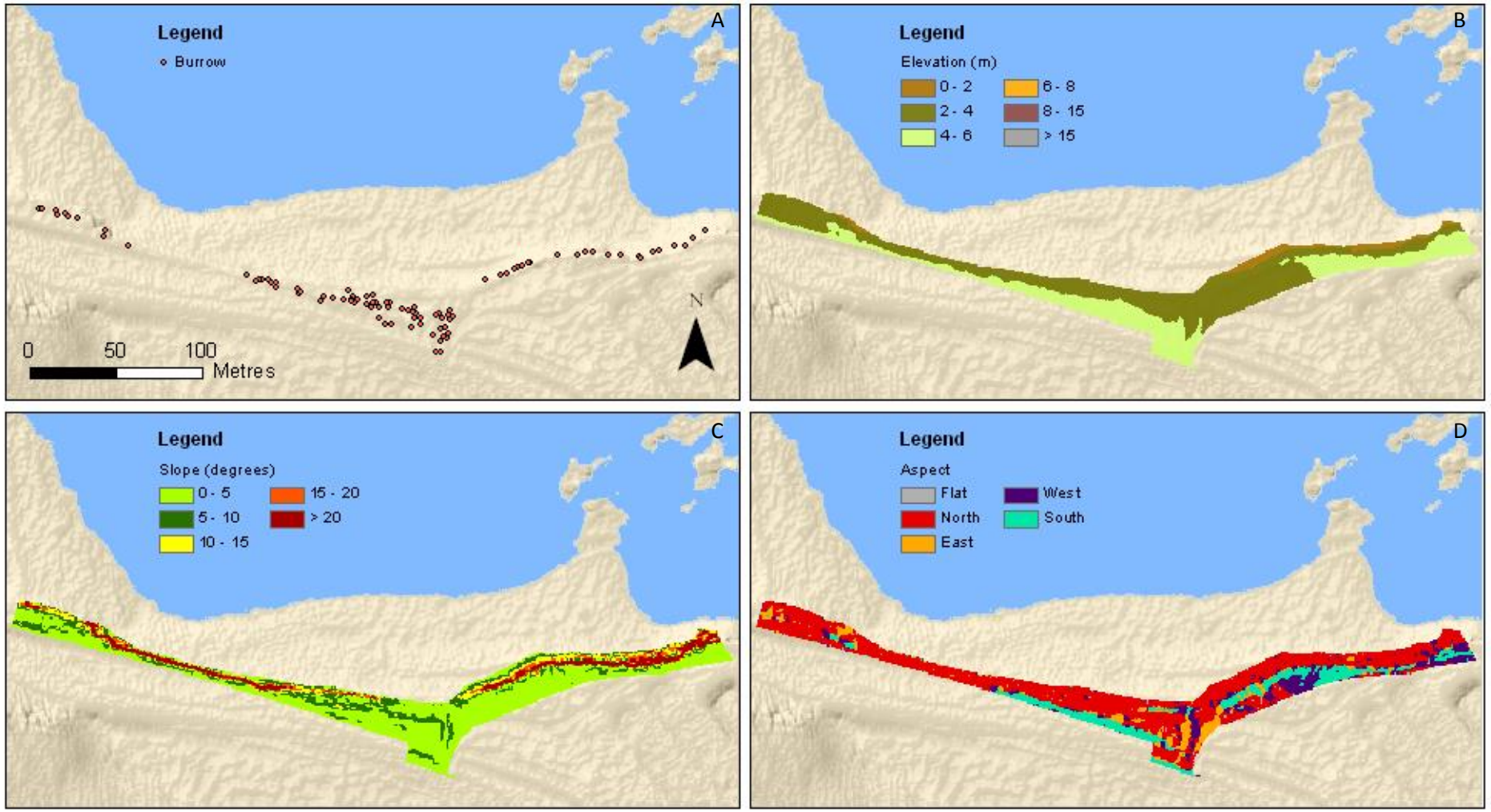


Figure 3-6 *Woody Point – A) Location of burrows, indicating a rectangular shape. B) Elevation of colony, most of the terrain is <4m. C) Slope – most 0-5 degrees. D) Aspect –north facing with some south facing terrain.*

The frequency of the terrain variables extracted from the DEM (*Slope, Aspect, Elevation and Solar radiation*) and *Distance to Coast* at each burrow point shows that few burrows were located on slopes > 20˚, or in areas of low solar radiation or with high wetness index. Burrows were found up to 48 m from the coast with the majority within 20 m of the coast due to the presence of a fence (Figure 3-8).

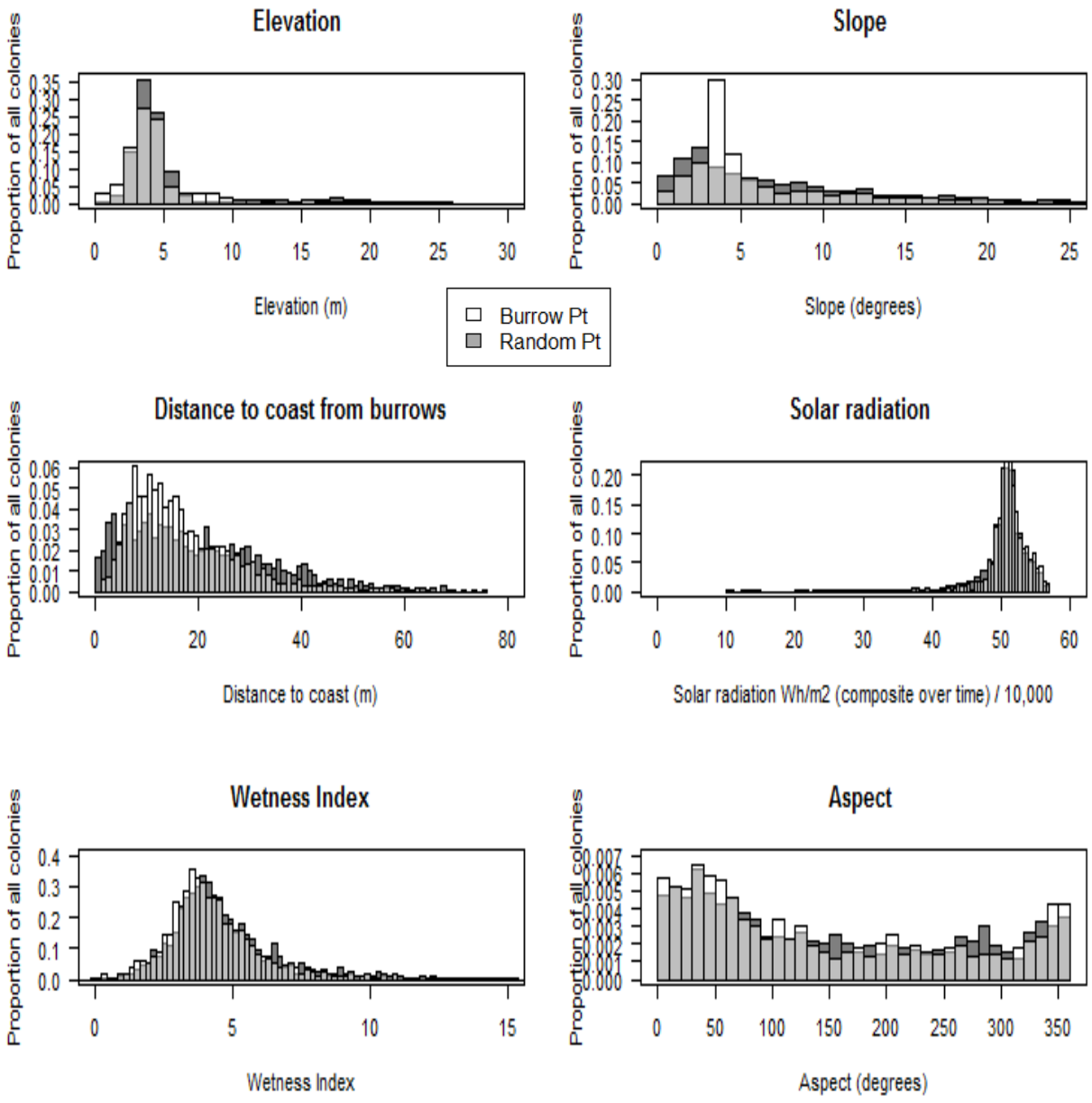


Figure 3-7 *Little penguin burrow frequency distribution against digital elevation model (DEM) variables across the six study colonies in NorthWest Tasmania. Burrow points are represented in white and a set of random points from one of the trials in dark grey. The overlap of the two sets is shown in light grey. The difference in slope indicates a much higher frequency of burrows in the 4 degrees category whereas the random points are more distributed across the range. The distance to the coast of the burrow points is also within 20 m whereas random points can be found up to 78 m away. The similarity of the profiles of both the burrow and random points indicates the colonies are narrow and fairly uniform throughout.*

3.4.2 Habitat suitability model

The model that best described the presence of burrows (*B*) included *Slope, Aspect, Solar Radiation* and *Wetness Index* (Table 3- 4). The selected model consistently appeared in the model selections with ΔAIC < 2 (Burnham & Anderson 2002). In this trial, AIC = 4569.2, AIC weight = 0.43183 (Table 3-4). The explanatory variables in the selected model had the most parsimonious AIC value on seven occasions, adding strength to the model's selection. (Appendix 3 contains summaries of all ten further trials). All terms were significant in the model: *Slope, Solar radiation* and *Windex ($p<0.001$)* and *aspect ($p<0.05$)* (Table 3-5). While the model explained the presence of burrows, a cross validation process used to test the model's predictive capacity indicated that the model was able to explain 62% of the variation for predicting the presence of burrows but only 42% for predicting their absence (Table 3-6).

Table 3-4 *Summary of generalised linear mixed-effect model (GLMM) comparisons with logit link and binomial response to analyse presence / absence of burrows. The top four models are shown along with the null model. B= burrow presence, Slope = log (slope) of cells, Aspect = the sin (aspect) of the cells, Solar = the amount of radiation from January – May, WIndex = the wetness index per cell. The random effect is the location (colony).*

Candidate models	Np	AIC	ΔAIC	wAIC
B~ Slope +Aspect + Solar + WIndex	**5**	**4569.2**	**0.0000**	**0.83949**
B~ Elevation+Aspect+Slope+Solar+WIndex	6	4571.2	1.9997	0.21485
B~ Slope+Solar+WIndex	4	4571.9	2.7604	0.14688
B~ Elevation+Slope+Solar+WIndex	5	4573.9	4.7561	0.05414
B~ (null)	1	4627.3	58.073	1.43192×10^{-13}

Np: number of parameters, AIC: Akaike's Information Criterion, **Δ**AIC: difference in AIC from that of the best fitting model, *w*AIC: AIC weight.

Table 3-5 *Results for the most parsimonious generalised linear mixed effect model (GLMM) characterising the effects of the terrain variables on habitat suitability of little penguin nest-sites. The best fit was determined according to the lowest Akaike's Information Criterion (AIC). The exp. (coefficient) provides the odds ratio.*

Variables	Variance	Estimate	SE	*z*	*P(>|z|)*	*Exp (coefficient)*
Fixed						
Intercept		-1.214	4.968 e-01	-2.444	<0.05	
Slope		-2.415 e-01	5.448 e-02	-4.432	<0.001	0.785
Aspect		1.160 e-01	5.321 e-02	2.180	<0.05	1.122
Solar		4.317 e-06	9.216 e-07	4.684	<0.001	1.000
WIndex		-1.189 e-01	2.043 e-02	-5.819	<0.001	0.888
Random						
Location	2.125e-13					
N_{obs}*=3335*						

Solar: Solar radiation, Windex: Wetness Index, SE: standard error, $N_{obs:}$ number of observations, Exp (coefficient): Exponentiate (coefficient).

Table 3-6 *Cross-validation results after 1000 trials for model B~ Slope +Aspect + Solar + WIndex.0 indicates absence and 1 indicates presence of burrow. The model has 62% accuracy in predicting presence (315 /473 trials) and 42% in predicting absence of burrows (221/527 trials).*

		Predicted values	
		0	**1**
Observed values	**0**	**221**	158
	1	306	**315**
% accuracy of selecting values from model		**42%**	**62%**

3.5 Discussion

Habitat suitability mapping based on small sample and plot sizes has been found to decrease the probability of accurately predicting a species distribution (Stockwell & Peterson 2002; McPherson *et al.* 2004; Pandit *et al.* 2010). The complete survey and mapping of burrows undertaken in six colonies should have led to an improvement in the predictive ability of the habitat suitability model. Precision was increased by the use of a DGPS in the recording of burrow location. The combination of the use of a DGPS in the field and very high resolution DEM has been shown to improve the accuracy of data incorporated into similar models (Van Niel & Austin 2007).

The chosen terrain variables (*slope, aspect, solar radiation* and *wetness index*) provided a habitat suitability model that was able to explain 62% of the distribution of little penguin nest-sites in the studied colonies. The use of terrain variables exclusively in a habitat suitability model allows a large amount of absence data to be randomly and repeatedly generated over several trials. This procedure strengthened the process and provided some robustness to the selected model. Terrain variables have been used to model habitat suitability for gorgonian corals (*Paragorgia aborea* and *Priminoa resedaeformis*) in North Atlantic waters (Tong *et al.* 2013), and stoat (*Mustela erminea*) activity in New Zealand which was associated with proximity to tracks, altitude, northerly and easterly aspect as well as topographical position and slope (Martin *et al.* 2011). Terrain variables that describe gradients to which plants are adapted have also been used in modelling the distribution of plant species. Altitude and topography were identified as the major factors influencing the distribution of vascular plants in the Cantabrian Range, Spain (Jimenez-Alfaro *et al.* 2014).

Penguins as a group are the only seabirds that approach the land directly from the sea, providing them with a different perspective of the topography than that from the air. It is quite possible that for little penguins, apart from proximity to foraging grounds, the visual cues provided by topography and terrain characteristics as seen in profile may play a role in the decision to select a colony and then a nest-site within that colony. The numbers of little penguins

returning to their colony is reduced in foggy conditions probably because of loss of orientation when visual cues are missing (Chiaradia *et al.* 2007).

Whilst no previous studies of seabirds have developed a habitat suitability model based on terrain variables only, these have been used in conjunction with other environmental variables, such as vegetation cover and soil type to explain species distribution. The nest density of blue petrel burrows was associated with slope and wetness index (Lawton *et al.* 2006), whilst that of sooty shearwaters (*Puffinus griseus*) and mottled petrels (*Pterodroma inexpectata*) was linked to increasing elevation and eastern aspect (Scott *et al.* 2009). For Eleonora's falcon *(Falco eleonorae)*, slope was most strongly associated with nest-site selection; however where the species was distributed on islands, distance to the coastline and incident solar radiation were of increased importance (Urios & Martinez-Abrain 2006; Kassara *et al.* 2012). Other examples where terrain variables have also been used include snow petrels *(Pagodroma nivea*) (Olivier & Wotherspoon 2005), and Adélie penguins (*Pygoscelis adeliae*) (Bricher *et al.* 2008).

In this study based on terrain variables alone, the best model predicted the presence of a nest-site 62% of the time. The model predicted that nest-sites occur on relatively high, north-facing slopes that receive high amounts of solar radiation as well as generally being drier than in other locations in the landscape. It is possible that the model could have included other variables that determine choice of nest-sites by burrowing seabirds. Vegetation for cover and the soil characteristics that determine cover were not considered as the data available were on a different scale.

Social interactions may also influence choice of nest-site, as could the distribution of access pathways. Temporal aspects that influence burrow occupancy might also influence model performance on a seasonal or annual basis. The model only predicted the absence of nest-sites in the colonies 42% of the time. Whilst this might indicate that suitable habitat remained unused, it could suggest that 58% of the variation is not being accounted for. Penguins might be expected to nest as close to the sea as possible in order to reduce the energetic costs in walking (Pinshow *et al.* 1977). They might also seek the appropriate combination of environmental variables to ensure suitable microclimatic conditions prevail at the nest-sites (Chapter 4).

Dry burrows are less likely to occur on south facing slopes or in valleys where the wetness index is high. As north-facing slopes in the Southern Hemisphere receive the most solar radiation, and hence a low wetness index, such slopes are the most likely to be selected. Interestingly, elevation was not a terrain factor required by the models. However, the maps (Figure 3-2B – 3-7B) indicate very little differentiation in the elevation present in these colonies; typically it was < 5 m. This is also clearly shown in the distribution of the burrow and random points (Figure 3-8E). Distance to the coast of nest-sites was also not a factor in the model and some penguins were found nesting up to 80 m inland (Figure 3-8e) or at the top of a headland (Figure 3-3), suggesting that the energetic costs were manageable over this distance and for reaching a high elevation, respectively. However, nest-sites were generally < 20 m from the coast,

peaking at between 6 - 8 m. This is much less than that found in a study on the Bass Strait islands where the peak distance was 20 m (Schumann, Dann & Arnould 2013), but reflected the presence of fence lines that hinder dispersal inland. Some nest-sites have also been discovered as far as 500 m inland at Phillip Island, Victoria (P.Dann pers. comm). Shallow slopes were the most favoured by little penguins, presumably because they increase the ease of digging of burrows, but nest-sites on level areas were also common.

The nesting habitat of seabirds is highly variable. Yellow-eyed penguin breeding areas are in thick vegetation at a mean distance of 500 m from the coast (Seddon & Davis 1989). Those of Magellanic penguins are influenced by thickness of vegetation but also by slope and substrate (Stokes & Boersma 1991, 1998). Skuas (*Catharacta spp*) nest in habitat with a north to north-west aspect in depressions with stable substrata (Quintana & Travaini 2000). Steep slopes, distinct spur-crests and a westerly aspect characterise the variables selected by the grey petrel (*Procellaria cinerea*) on Macquarie Island (Schulz *et al.* 2005). Single variables or a combination of variables can be correlated with the presence of seabirds on islands (Schumann, Dann & Arnould 2013). Distance to the coast, slope and proportion of vegetation cover were important for the common diving petrel (*Pelecanoides urinatrix*), whereas distance to coast was the only variable determining the distribution of little penguins on some of the Bass Strait islands (Schumann, Dann & Arnould 2013). This contrasts with the findings in the present study where distance to the coast was not one of the determining factors in the model. Perhaps a lack of competition for nests in these study colonies meant that the distance to coast was less significant; as well as restriction of the movement of birds inland.

Spatial heterogeneity of seabirds' nest-sites may reflect the adaptability of species to different conditions, or the selective advantage of different burrow sites under contrasting conditions. The variety of nest-sites used by little penguins suggests that they are generalists in their selection and even opportunists, as they readily make use of artificial nest-sites. This also suggests that there is no "ideal" nest environment and that any good quality habitat is suitable for breeding. "Good quality" habitat refers to the ability of a given environment to provide the appropriate conditions for individual and population persistence. Hence habitat quality should be explicitly linked to survival and reproduction rates, rather than vegetation features (Hall *et al.* 1997). This has implications for conservation and management in this study, as colonies that support many high-cover weed species, such as honeysuckle *(Lonicera periclymenum*), cape ivy *(Delirea odorata)* and rambling dock *(Acetosa sagittata),* still contain many locations that little penguins use as nest-sites.

Chapter 2 proposed that many of these colonies could be fragments of a larger colony that has come under anthropogenic pressure, in this instance road, rail and invasive predators leading to shifts over time to other area with less pressure. This may also involve the Allee effect whereby past colonies have crashed when the numbers have reached a critical minimum threshold. Whether little penguins demonstrate the Allee effect is still to be determined, though

the quality of habitat patches has been shown to have an influence (McVinish & Pollett 2013). The availability of suitable habitat in other areas of the coast still needs to be examined. A longer-term study would be required to assess whether the selective advantage of different burrow types changes with inter -annual changes in climate.

This study has demonstrated that terrain variables derived from high resolution DEMs can be used successfully in a model that describes the location of nest-sites. High resolution DEM's are becoming increasingly available and provide data that is now comparatively easy to access and use than data collected in the field. Terrain variables contributed to the habitat suitability model of little penguins and a similar process could be used with other seabird colonies. Terrain variables may also assist conservation and management planning of habitats for little penguins in peri-urban and coastal areas.

CHAPTER 4

Comparison of temperature and relative humidity in natural and artificial burrows of a burrowing seabird, the little penguin (*Eudyptula minor)*, in semi urban colonies

4 Comparison of temperature and relative humidity in natural and artificial burrows of the little penguin (*Eudyptula minor)*

4.1 Abstract

Microclimate is an important property of burrows that are used by many animals, including some seabirds that need to return to land to breed and moult. Appropriate microclimatic conditions in the nest-site or burrow mean that more energy resources can be invested in growth rather than thermoregulation. This study investigated the thermal properties of grass, vine, sand and artificial burrows used by little penguins (*Eudyptula minor)* during the chick rearing and moulting seasons. The thermal properties of these different types of nest-sites, both those roofed by vegetation and those below ground, were quantified using the hourly variation of temperature and relative humidity and the relationship between the internal burrow temperature and the outside colony temperature. The microclimate of artificial burrows was 1.4˚C higher in temperature and 10% lower in relative humidity than in natural burrows. Further, the frequency of readings exceeding the Upper Critical Temperature (UCT > 27˚C), was highest in the artificial burrows. Of the natural nest-sites, those roofed by grass sites remained relatively cooler at higher temperatures and relatively warmer at cooler temperatures, and the temperature rarely reached the UCT. Artificial nest-sites are widely used to supplement natural nest-sites in seabird colonies around the world. The potential for climate warming to increase the frequency of UCTs during critical phases of the breeding cycle may need to be taken into account in the future design and deployment of artificial nest-sites.

4.2 Introduction

Many animals use burrows for some aspect of their life history. Enclosed cavities, nests and burrows are mainly used for breeding and protection from predators; however, they also provide a means of protection from extremes in climate. Burrows, from deserts and semi-arid environments to the poles, can therefore assist animals with thermoregulation. In some cases they are used as a food source; for example, aardvarks (*Orycteropus afer*) that live in semi-desert environments use the buffered cooler temperatures and higher humidity of their burrows to germinate seeds for food (Whittington-Jones *et al.* 2011). Merriam's kangaroo rats (*Dipodomys merriami*) modify the entrances to their burrows in subtle ways to optimise the microclimate within the burrow during the year (Tracy & Walsberg 2002; Edelman 2011). While some animals inhabit burrows on a permanent basis, for example pocket gophers (*Rodentia: Geomyidae*) (Roberts *et al.* 1997) and silvery mole rats in Malawi (*Heliophobius argenteocinereus*) (Sumbera *et al.* 2004), others use them temporarily for breeding, shelter and/or hibernation (Hazard & Morafka 2004; Jurczyszyn 2007; Belovezhets & Nikol'skii 2012).

The vast majority of seabirds nest on land in colonies and many species use burrows for breeding and moulting. Burrows can be under the substrate, above ground on the surface, or under vegetation. Seabirds breeding above ground use nests that are open to ambient conditions

and therefore potentially exposed to climatic extremes. Those using covered nest-sites or burrows can take advantage of the modified microclimates as they offer the potential to improve breeding success. While most penguins nest in the open, particularly in the higher latitudes, those breeding at lower latitudes tend to use burrows. Four species of penguins which span a wide geographic range, African (*Spheniscus demersus*), Humboldt (*Sphensicus humboldti*), Magellanic (*Spheniscus magellanicus*) and little penguin (*Eudyptula minor*) habitually burrow.

Little penguins are found across more than 10^{o} of latitude in Australia and New Zealand, in areas that regularly experience frost to those where ambient air temperatures can exceed 30^{o}C (Klomp *et al.* 1991; Fortescue 1995; Ropert-Coudert *et al.* 2004). However, their actual distribution is generally limited to regions with mean sea temperatures above 10^{o}C (Stahel & Nicol 1982). Given this wide geographic range, little penguins exhibit inter-population variability in several aspects of their physiology, ecology, morphology and genetics (Overeem *et al.* 2008; Peucker *et al.* 2009).

Little penguin nest-sites can be a burrow below ground in the substrate, or above ground under vegetation. Hereafter "nest-site" will refer to both burrow types. Nest-sites within the substrate are dug into the sand, soil or cavities among rocks along the coast; some penguins also use caves (Klomp *et al.* 1991; Soto-Gamboa *et al.* 1999). Nest-sites under vegetation are simply openings under the branches and foliage of shrubs, grasses and vines. As the structural complexity of the vegetation is likely to affect the extent of circulation of air through the nest-sites, different microclimatic conditions might prevail in those below and above ground. Below ground, ventilation and the circulation of air is driven by the gradients between the substrate and the atmosphere (Ganot *et al.* 2012).

Modification of the landscape by urban encroachment and other human activities often leads to a lack of suitable habitat for nest-sites. In such situations, birds can make use of buildings and other man-made structures (drains, pipes *etc*). This has also led to the increasing use of artificial nest-sites and nest boxes as a conservation and management tool to mitigate the loss of natural habitat. They have been used for a wide range of birds: African penguins (Kemper *et al.* 2007; Sherley *et al.* 2012), Eurasian rollers (*Coracias garrulus*) (Rodriguez *et al.* 2011); tree swallows (*Tachycineta bicolor*) (Ardia *et al.* 2006), Baya weavers (*Ploceus philippinus*) (Asokan *et al.* 2008), American kestrels (*Falco sparverius*) (Butler *et al.* 2009), mallards (*Anas platyrhynchos*), blue winged teals (*Anas. Discors*) (Gloutney & Clark 1997), Madeiran storm petrels (*Oceanodroma castro*) (Bolton *et al.* 2004), Mediterranean storm petrels (*Hydrobates pelagicus melitensis*)(Libois *et al.* 2012) and Gould's petrels (*Pterodroma leucoptera leucoptera*) (Priddel *et al.* 2006). In general, artificial nest-sites might be expected to have different thermal masses and hence vary more in temperature and humidity in comparison to natural sites.

Artificial nest-sites and nest boxes used in penguin colonies around the world are made of a variety of materials: wood, fibreglass, plastic and concrete, all of which have very different

thermal properties. Well-designed artificial nest-sites allow a better chance of survival of nesting birds and their young and can provide more protection from predators. Microclimate of cavities or burrows has been investigated for lesser kestrels (Catry *et al.* 2011), African penguins (Lei *et al.* 2014) and little penguins (Ropert-Coudert *et al.* 2004).

The thermal properties of nest-sites influence the thermoregulatory ability of individuals, and ultimately their energy budgets and heat stress levels. The thermal neutral zone (TNZ) is the zone of temperatures where the metabolic activities of mammals and birds remain constant (Porter & Kearney 2009). For little penguins in Tasmania, this has been found to vary between 10 - 30^{o}C (Stahel & Nicol 1982). Recent work by Horne (2010) found that the thermal neutral zone (TNZ) of little penguins varied among colonies around Australia (Table 4- 1). The thermal neutral zone has been shown to decrease as latitude increases (Table 4-1). There does however seem to be a degree of plasticity in these values.

Table 4-1 *Thermal Neutral Zone in Australian little penguin colonies, with comparative data for two other penguin species.*

Species	Location	Latitude & Longitude	Thermal Neutral Zone	Reference
Little penguin *Eudyptula minor*	Penguin Island	32.35^{o}S, 115^{0}E	12 - 30^{0}C	Horne (2010)
Little penguin *Eudyptula minor*	Kangaroo Island	36^{o}S,137.6^{0}E	12 - 30^{0}C	Horne (2010)
Little penguin *Eudyptula minor*	Phillip Island	38.5^{o}S, 145.2^{0}E	6 - 27^{0}C	Horne (2010)
Little penguin *Eudyptula minor*	Hobart, Tasmania	42^{0}S	10 - 30^{0}C	Stahel & Nicol (1982)
Humboldt penguin *Spheniscus demersus*	na	na	2 - 30^{0}C	Williams (1995)
Emperor penguins *Aptenodytes patagonicus*	na	na	-10 – 20^{0}C	Williams (1995)

na: not available in literature

Temperatures above the upper critical temperature (UCT) i.e. > 27^{o}C increase metabolic activity in little penguins though this is dependent on the gradients of temperature between the body of the bird and the environment (Calder & King 1974; Horne 2010). Thermoregulation in little penguins principally involves cooling either: from increasing blood flow to peripheral structures such as flippers, feet and head to increase heat loss (Groscolas 1988) or panting (Stahel & Nicol 1982). Adjustments to postural positions such as holding flippers away from the body, stretching out the neck and stretching their feet behind them, increase surface area to volume ratio and assist in maximising heat loss (Murrish 1973; Calder & King 1974).

Temperatures above UCT may adversely influence the incubation of eggs and, because of their size, the chicks' ability to thermoregulate. The survival of moulting penguins during the hottest part of the season whilst they are on land may also be negatively affected. (Dann & Chambers 2013). Little penguins are able to cope with heat exposure in the short term, but issues with hyperthermia and / or respiratory alkalosis are likely if heat exposure is prolonged (Murrish 1982, 1983). Chicks are poikilothermic when they hatch, but develop the ability to thermoregulate within 10 days; so they are more vulnerable to heat stress whilst poikilothermic (Williams 1995).

This study investigated the thermal properties of vegetation, sand and artificial nest-sites at micro temporal scales. The specific aims and associated null hypotheses (H_o) were to:

(i) examine the variation in temperature and humidity within each nest-site type and to quantify the differences in temperature and relative humidity among the types of nest-sites;
(Ho): there is no difference in the variation of temperature and humidity among the types of nest-sites.

(ii) identify the relationship between the internal nest-site temperature and the outside colony temperature for each nest type;
(Ho): there is minimal difference between the inside and outside temperature among the types of nest-sites

(iii) investigate whether nest-site temperatures reach the Upper Critical Temperature (UCT) and if so, which categories of nest-sites are more predisposed to reach the UCT.
(Ho): all nest-sites reach UCT in equal amount of times

4.3 Method

4.3.1 Study Sites

Two little penguin colonies on the North West Coast of Tasmania were used as the study sites (Figure 4-1). These two colonies were part of the mapping study in Chapter 2. The proximity and variety of nest-sites available at these two colonies made the sites suitable study areas.

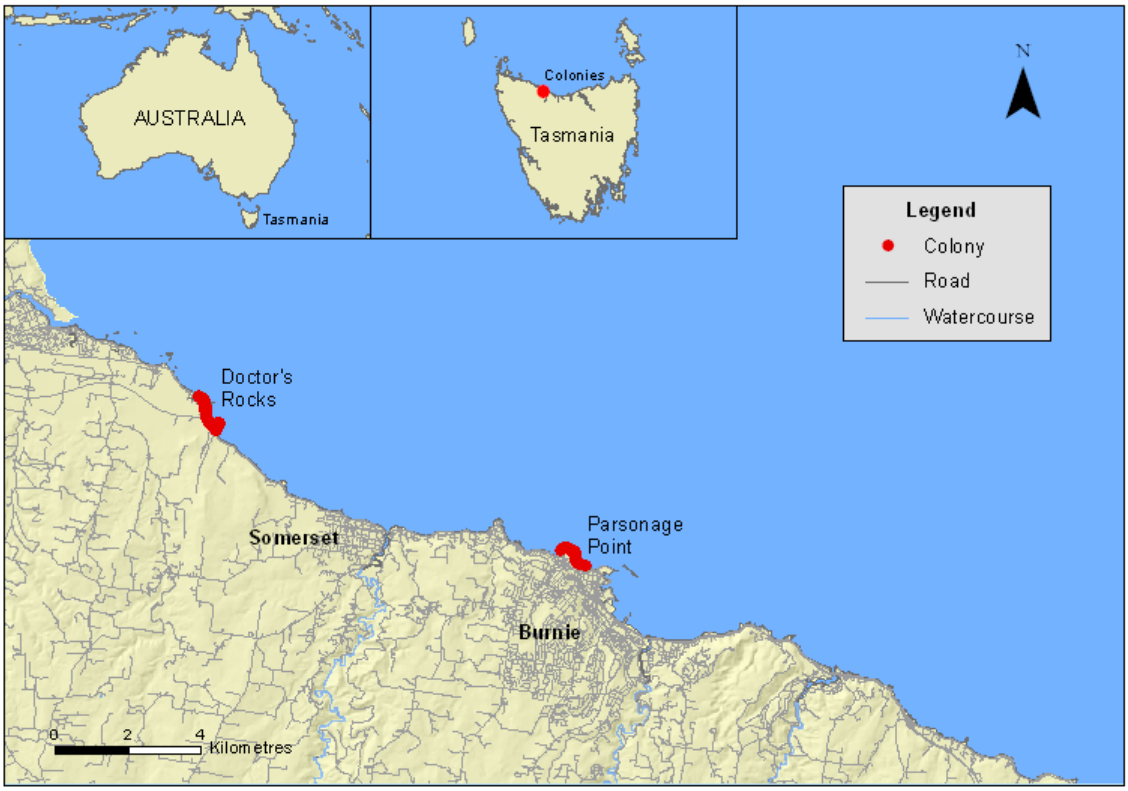


Figure 4-1 *The location of the two little penguin colonies on the North West Coast of Tasmania, Australia; Doctor's Rocks and Parsonage Point*

The Doctor's Rocks colony (-41.00ºS 145.77ºE) near Wynyard is about 1 km in length and composed of a variety of vegetation ranging from shrubs (mostly *Correa* sp, tea tree sp) to tussocks (*Poa* sp., *Tetragonia* sp.). It contains vegetation nest-sites (grasses and vines), substrate (mostly sand) nest-sites, and some artificial nest-sites that were placed here in the early 2000s. The colony is divided into two areas: a beach area covered with grass and shrubs, and an area covered in vines, shrubs and trees. These areas are separated by a rock face and are approximately 100 m apart.

The second colony, 12 km to the east at Parsonage Point **(**-41.04 ºS 145.89 ºE) in Burnie is 800 m in length and is a headland that consists of old landfill building material that has been revegetated, but supports mostly grasses and shrubs with very little substrate for nest-sites. From anecdotal accounts, penguins have inhabited this area since at least the 1960s. Fencing of the colony took place in 2002, which restricted access to other areas previously used for nesting by

penguins. To increase the availability of habitat, artificial nest-sites, in the form of concrete igloos, were added to the colony around that time. These sites have been used successfully for breeding since 2000 (P.Marker, pers. comm.)

A variety of burrow types were actively in use by penguins within these two colonies. The types were classified as sand, grass, and vine or artificial. Other burrow types were found under shrubs. The shrubs varied from 1 m to 2 m in height, and were of various widths. As they were often very difficult to access, shrub nest-sites were omitted from the experimental design. Thus micro-scale comparisons of the microclimate of three types of natural burrow and one type of artificial burrow were undertaken (Table 4-2). All the artificial nest-sites used in this study were "igloo-shaped" and made of concrete, either with or without ventilation holes, and sometimes covered in vegetation (termed igloos).

Table 4-2 *Summary of burrow types and number of iButtons (data logger) used in this study. Doctor's Rocks little penguin colony was divided into two areas: one part covered in vines, shrubs and trees (1); the second area was focussed on a beach area covered with grass and shrubs (2). The two were separated by a rock face and were 100 m apart.*

Colony	Type of nest-site Below ground (B) or above ground (A)	Definition	Number of iButtons used in nests n	Number of iButtons used to measure air outside the burrows temperature (T) and humidity (H)
Doctor's Rocks (2)	Sand (B)	No vegetation used in the construction of the burrow.	n = 12	
Doctor's Rocks (2)	Grass (A)*	Long strappy blades of varying thickness that overlap each other.	n = 13	T= 8 H = 3
Doctor's Rocks (1)	Vines (A)*	Climbing, twining, winding or sprawling plants, usually with a woody stem.	n = 17	T= 6 H = 2
Parsonage Point ** Doctor's Rocks (1)	Artificial (A)	Artificial structures that are made from concrete and look like igloos in most cases. Three sub categories: Artificial – with holes Artificial – no holes (nh) Artificial - Igloo	n = 14 – Artificial n = 7 - Artificial_nh n = 3-Artificial igloos**	T= 9 H = 4

4.3.2 Temperature and humidity

Thermocrom iButton DS 1921G loggers (resolution: 0.5^{o}C, 17.35 x 5.89 mm) and DS1923 Hygrochron iButton loggers (temperature resolution to 0.5^{o}C and relative humidity (RH) to 0.04% RH, 17.35 x 5.89 mm) (Dallas Identification/Alfa-Tek, Bayswater, Victoria, Australia) were used in this study. The loggers were placed in a fob (a black plastic holder) and attached with adhesive tape to a 5-cm decking screw which was pushed into the roof or side of the nesting

chamber. Care was taken to ensure that loggers did not touch any part of the nest-site surface. The loggers (Thermocrom iButtons) were set to record temperature and, where available, relative humidity (Hygrochron iButtons) every hour (Table 4.2).

The natural nest-sites were selected at random throughout the colony, but only those with chambers that were approximately 1 m or less in length were used. This was done to measure comparability with the artificial burrows that were all approximately 900 mm in length. Most natural nest-sites were approximately 1m in length. Comparison of types of natural burrows of varying lengths was not possible due to logistic limitations on the correct placing of the logger in smaller burrows or burrows greater than 1 m.

The ambient air temperature of the colony (colony air temperature) outside the nest-sites was logged simultaneous at hourly intervals using iButtons attached at a height of 20 cm to a wooden stake and placed facing south with a wooden cover to shade the logger from the weather and direct solar radiation (Table 4.2). No monitored nest-site was more than 10 m away from a colony air temperature logger.

The loggers were deployed between 24th January 2012 and 28th March 2012, during the hottest part of the summer. This season coincides with the part of the breeding cycle when chicks are present and the moulting season. The hourly recordings were categorised as day and night according to sunrise and sunset hours (*Maptools* package in R).

4.3.3 Statistical analysis

The data from the iButton loggers were downloaded using the Express Thermo Software (Dallas Identification/Alfa-Tek, Bayswater, Victoria, Australia). The data from all loggers was analysed using the R statistical environment (R Core team 2013).

The ambient air temperatures and relative humidities from each of the three areas were averaged by day and night for each burrow in each type of burrow category. This was then graphed. For all the other following models the entire data set of temperatures was used.

4.3.3.1 Colony variation of air temperatures

To investigate the effect of the location of the colonies on variation in temperature, a comparison of the air temperatures among the three areas: Doctor's Rocks (1) n = 6, Doctor's Rocks (2): n = 8 and Parsonage Point: n = 9 was undertaken using a generalised linear mixed effects model (GLMM) which used the *lme* function (package *nlme*). The response term (the ambient air temperature of the colony) was fitted with REML with time of day and location as fixed terms and the air temperature of the colony as the random term.

*Model 1: Air temperature of colony ~ location * dn +1| Air temperature Id*

Where *Location* refers to the colony (Doctor's Rocks areas (1) and (2) and Parsonage Point); *dn* refers to the day/night temperatures. These were the fixed terms with the *Air temperature Id* (the iButtons measuring the colony temperature outside the burrows) as the random term.

4.3.3.2 Inter comparison of microclimate of burrow types

A GLMM was fitted to the data to investigate the temperature of the burrows (response variable) with the interactions of fixed factors (*Burrow type, time of day (day/night)*), and random factors (*Burrow*) nested in Colony *(Location).*

*Model 2: Temperature of burrow ~ Burrow Type * day/night + 1| Location / Burrow Id*

A similar model was used for the relative humidity (which required log transformation) response variable with interactions of fixed (Burrow type, time of day (*day/night)*) and random (Burrow (*Burrow)*) factors nested in Colony *(Location).*

*Model3: Log (Relative humidity of burrow) ~ Burrow Type * day/night + 1| Location / Burrow Id*

4.3.3.3 Relationship between colony temperature (T_o) and burrow temperature (T_i)

Temperature difference (T_d) defined as the difference between the temperature inside (T_i) and outside (T_o) the burrow.

$$T_d = T_i - T_o$$

A positive T_d indicates the temperature inside the nest-site was higher than the temperature outside the nest-site. To investigate how T_d influenced heating and cooling over time, a GLMM was used to model T_d (response variable) against the interaction of type of burrows and during day and night, and random factors (Burrow (*Burrow*)) nested in Colony *(Location).*

*Model4: Td ~ Burrow Type * day/night + 1| Location / Burrow Id*

4.3.3.4 Upper Critical Temperature (UCT)

Above the upper limit of the thermal neutral zone, heat loss must increase to maintain the metabolic stability of the penguin. An Upper Critical Temperature (UCT) of 27^{o}C was used in this study as the indicator for UCT for North West Tasmania rather than 30^{o}C used for penguins in the south of the state, as the study site is approximately half way between Phillip Island, Victoria and Hobart, Tasmania (Table 4-1).

A Generalised Linear Model (GLM) was fitted to the proportion of temperatures > 27^{o}C for each burrow type.

Model 5: Percentage >27^{o}C~ Type of burrow

All statistical analyses were performed in the R statistical environment (R Core team 2013).

4.4 Results

4.4.1 Colony temperature

The average day temperatures were: Doctor's Rocks (1) 19.2ºC ± 0.3, Doctor's Rocks (2) 22.9 ºC ± 0.2 and Parsonage Point 21.7ºC ± 0.2. The average night temperatures were; Doctor's Rocks (1) 14.2ºC ± 0.3, Doctor's Rocks (2) 13.6 ºC ± 0.2 and Parsonage Point 15.4ºC ± 0.2. Over the study period, the colony air temperature decreased, with the maximum temperatures in January (during the chick rearing season) and the minimum temperatures in March (moulting season) (Table 4-3).

Table 4-3 *Summary of maximum and minimum colony (ambient air) temperatures and relative humidity obtained in North West Coast colonies. Dates and times are shown when these maxima and minima were recorded. In addition, where these values were obtained more than once, a percentage occurrence is given in brackets below.*

Colony	Max Temp ºC	Min Temp ºC	Max relative humidity %	Min relative humidity %
Doctor's Rocks (1)	30.5 25/2/2012 1.00 pm	2.2 24/3/2012 1.00 am	100 ~4 - 27/3/2013 (3.5%)	32.8 26/1/2012 1.00am
Doctor's Rocks (2)	37.2 29/1/2012 4.00 pm	0.5 24/3/2012 1.00 am	100 ~4 - 27/3/2012 (4.3%)	20.8 28/2/2012 4.00pm
Parsonage Point	32.7 26/1/2012 3.00 pm	5.5 24/3/2012 2.00 am	100 ~4/3/2012 (0.58%)	24.5 25/1/2012 7.00pm

A box and whisker plot of both temperature and relative humidity Figure 4-2 illustrates the variation within each group of burrows over the time of the survey.

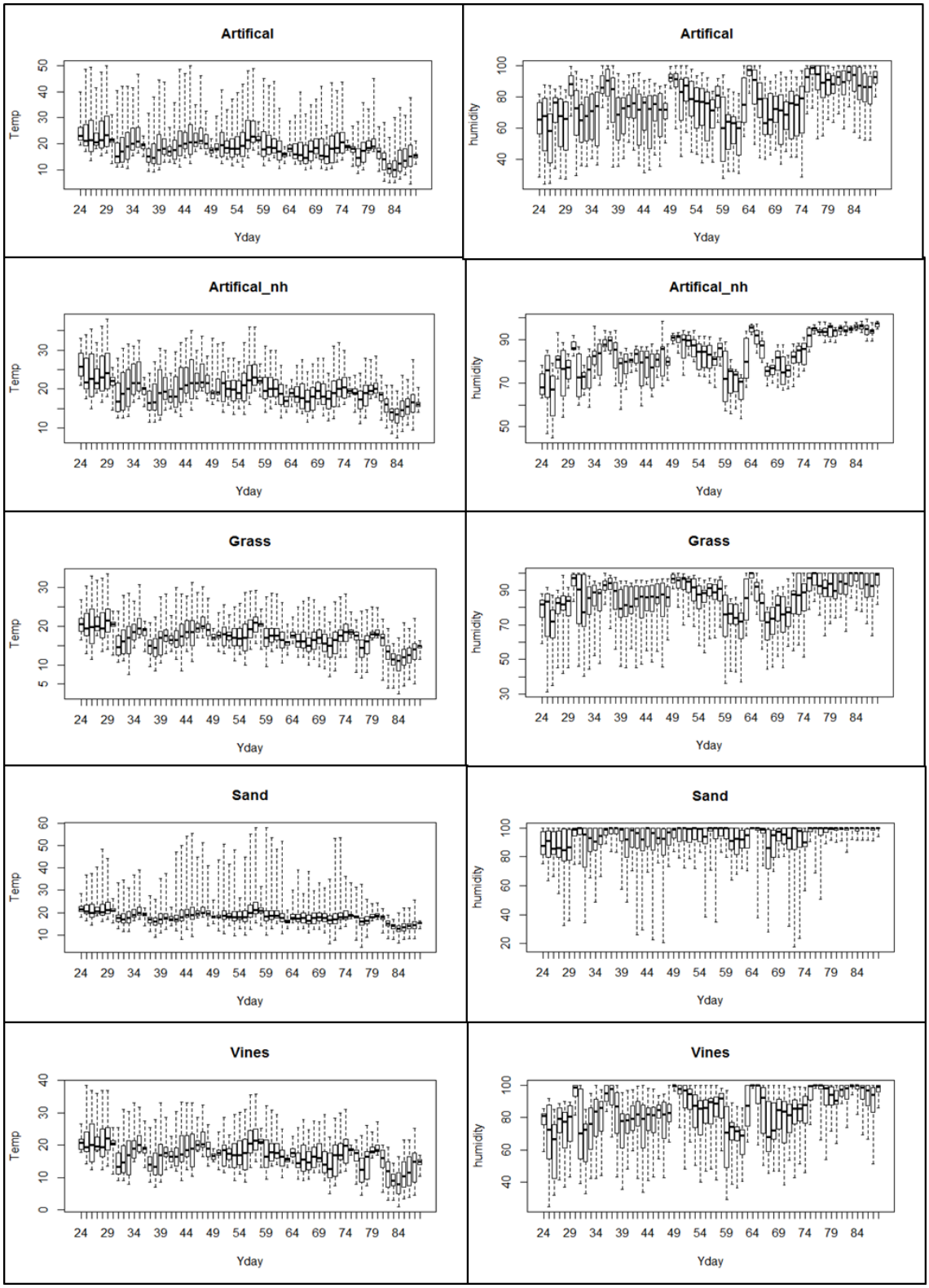


Figure 4-2 *Temperature and humidityreadings of different little penguin burrow types. Each group of burrows is summarised over each day of the recording of data. Yday refers to the Julian Day number after 1 January; the data were collected from January 24th (Julian Day 24) until March 28th (Julian Day 88). The thick black line of each box is the mean with the lower and upper quartiles shown. The range of upper and lower limits are indicated by the dashed lines. Temperature and humidity values of burrow type are shown alongside each other.*

Results of the Model 1 analysis indicated that the air temperatures in the three areas were significantly different from each other ($F_{(2,35440)} = 424.77$, $p<0.0001$).

Microclimatic differences were present between the sites at the 10-100 m scale. The day temperatures varied more among sites than the night temperatures (Figure 4-3) suggesting that variation in insolation is mainly driving the site-to-site differences.

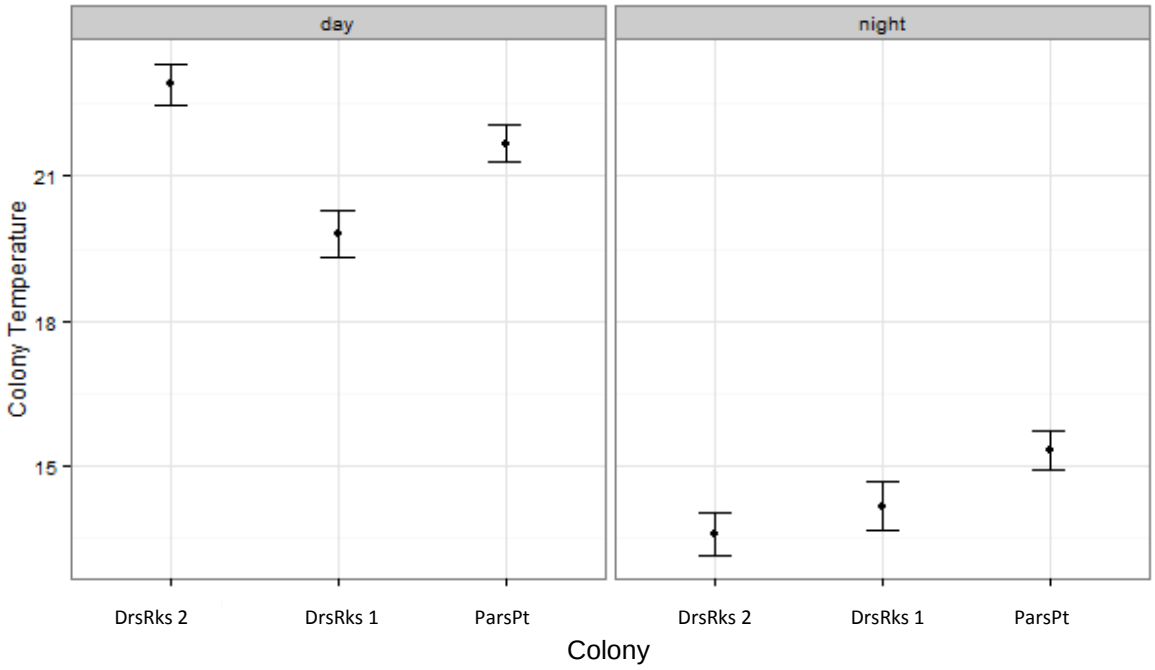


Figure 4-3 *Average colony air temperature plotted among the three areas ± SE. The mean colony air temperature of DrsRks2 (Doctor's Rocks 2) is 3ºC higher than the DrsRks(Doctor's Rocks 1) area, while there is 1.5ºC difference between ParsPt (Parsonage Point) and the two Doctor's Rocks areas. At night, there is much less difference between the temperature values.*

4.4.2 Variation of temperature and humidity among burrow types.

Vine and grass burrows were the coolest, with mean temperatures of 17.2ºC ± 1.2 SE and 17.2ºC ± 1.1 SE, respectively (Table 4-4). Sand burrows had a mean of 18.6ºC ± 1.3 SE. Artificial burrows with no ventilation holes were the warmest (19.8ºC, 1.8 SE); artificial burrows with ventilation holes had slightly lower average temperature (19.2ºC ± 1.6 SE).

Sand burrows were consistently the most humid (mean 93.4%, ± 5.4 SE) whereas the artificial burrows overall (with holes, no holes and vegetation covering) maintained the lowest average humidity (77.2% ± 7.4 SE). This suggests that the insulation and thermal properties of the burrows vary and influence their microclimate.

Table 4-4 *Comparison of mean ± SE of temperature and relative humidity by burrow type for little penguins. There are no relative humidity values for igloos (Artificial burrows with vegetation covering) as the loggers could not be retrieved. Vine and grass burrows have the lowest average temperatures, whilst artificial burrows have the lowest relative humidity.*

Burrow type	Average Temp ºC±SE	Number of burrows (n)	Average Relative Humidity % ± SE	Number of burrows (n)
Artificial	19.22 ± 1.63	14	77.18 ± 7.41	5
Artificial - no holes	19.76 ± 1.82	6	na	na
Artificial - veg	18.22 ± 2.74	3	na	na
Igloo				
Grass	17.18 ± 1.06	13	85.22± 7.38	3
Sand	18.60 ± 1.26	12	93.44 ± 5.36	4
Vines	17.15 ± 1.22	17	83.51 ± 7.96	4

4.4.3 Inter comparison of burrow types

The GLMM used to model the effect of temperature as the response variable, Model 2 ($F_{(5,100012)} = 348.413$ $p < 0.0001$) indicates that the temperatures are significantly different among all groups. For the effect of relative humidity (log transformed) as the response variable, Model 3 ($F_{(4,24652)} = 184.42$ $p < 0.001$) shows that burrow categories were significantly different. The effect of temperature and relative humidity on the interaction of type of burrow and time of day is shown in Figure 4-4.

There were clear differences between day and night temperatures for all burrow types. The biggest change of 6°C occurred in artificial burrows with holes; these also had the highest day temperatures. Artificial burrows with holes maintained the highest temperature during the night and second highest during the day. Of the natural burrow types, sand burrows maintained the highest temperatures during the night, reflecting the high thermal capacity of sand and the greatest difference between day and night temperatures was for vine burrows. Relative humidity was higher at night than day for all burrow types. Sand burrows consistently maintained the highest values, > 90%.

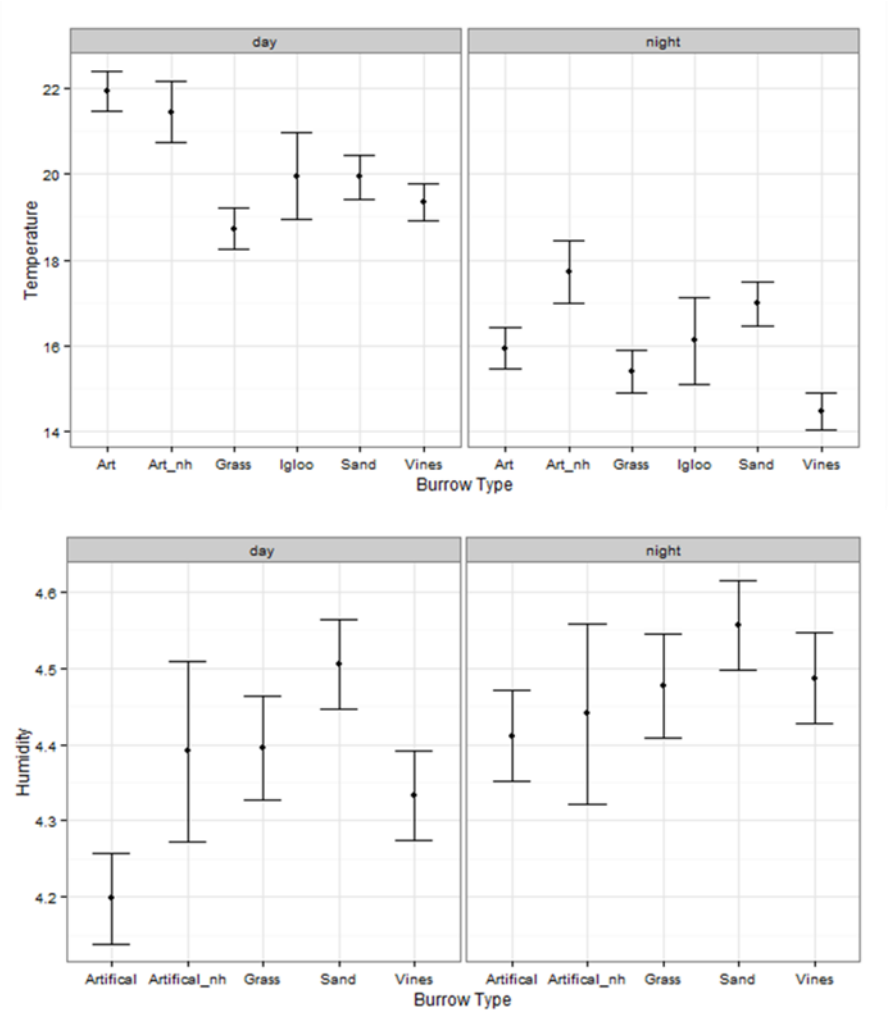


Figure 4-4 *Temperature (± SE) and relative humidity (log transformed) (± SE) from a GLMM of little penguin burrow categories during day and night. The types of burrows are artificial with holes (Artificial), no holes (Artificial_nh), with vegetation covering (Igloo) and Sand, Grass and Vine. There were no relative humidity recordings for the igloo burrows.*

4.4.4 Relationship between colony temperature (T_o) and burrow temperature (T_i)

Figure 4-5 illustrates the difference between burrow and ambient colony temperatures (T_i-T_o) against the colony temperature (T_o) recorded at every hour for the duration of the experiment. The clouds of points represents all the readings of all the loggers and provides insights into the thermal properties of the burrows. Figure 4-6 shows the fitted plots of the differences between burrow and ambient colony temperatures (T_i - T_o) during day and night for all the burrow types.

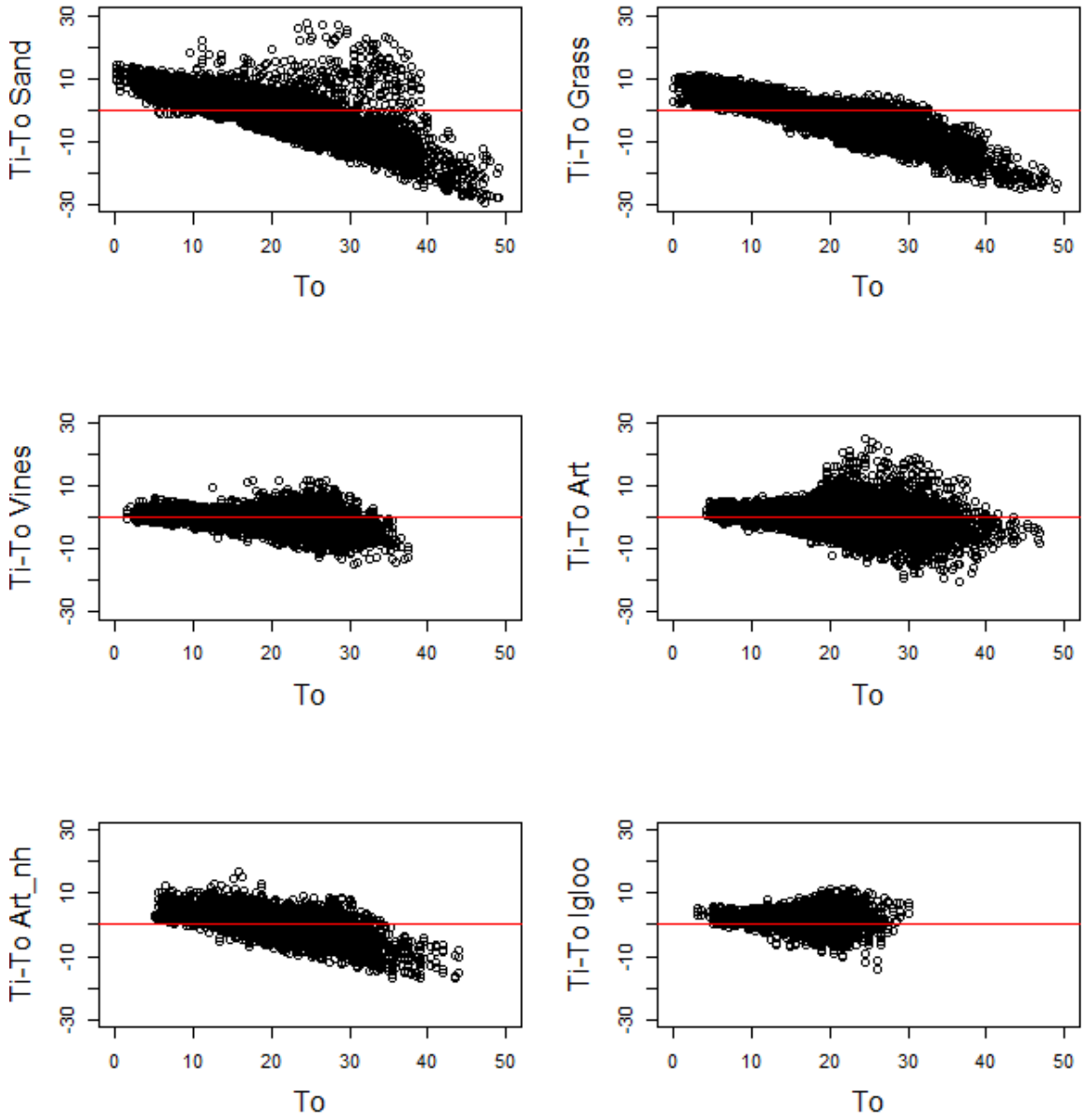


Figure 4-5 *Plots of all values of $T_d = T_i$-T_o values against T_o readings in all little penguin burrow categories. Positive differences (values>0) indicate that the burrows were warmer than the colony temperature, whereas negative differences indicate the burrows were cooler than the colony temperatures. Grass and sand burrows tended to be warmer ie $T_i > T_o$ at lower temperatures and cooler ie $T_i<T_o$ at higher temperatures. Grass burrows had smaller differences on the positive side. Vine burrows maintained temperatures with very little difference T_d values tended to be between -10 ^oC - 10^oC indicating that these burrows are not significantly warmer or cooler than the colony temperature Artificial burrows (with holes) appeared to fluctuate much more around the 0^oC difference T_d. Artificial burrows (with holes) appeared to be similar to grass burrows. The small number of artificial burrows with vegetation accounts for the smaller cloud of points.*

There was a significant two-way interaction between burrow type and time of day (Model 4 results; $F_{(5,100000)} = 174.52$ $p < 0.001$).

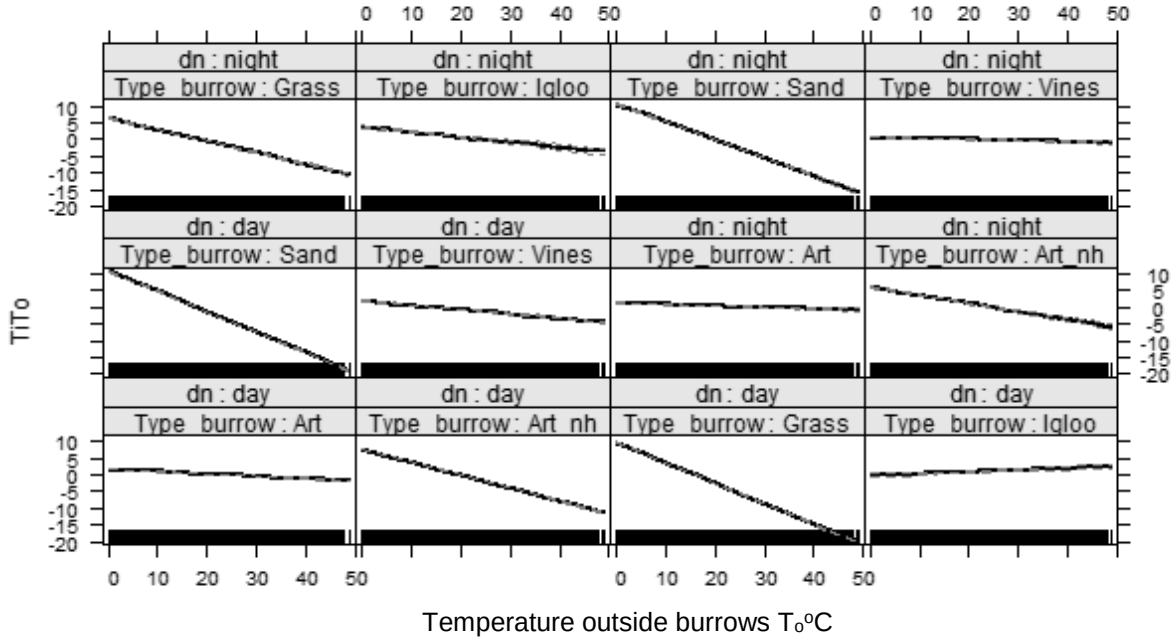


Figure 4-6 *Fitted plots of all $T_d = T_i - T_o$ values against T_o readings in all little penguin burrow categories during day and night. Positive differences (values>0) indicate that the burrows are warmer than the colony temperature, whereas negative differences indicate the burrows are cooler than the colony temperatures. The differences between day and night temperatures of each burrow type are small. Of note is the similar trends in grass and sand burrows where there is a strong tendency to be warmer (i.e. $T_i > T_o$) at lower temperatures and cooler (ie $T_i < T_o$) at higher temperatures during both day and night.*

4.4.5 Upper Critical Temperature (UCT)

The GLM that was fitted to the proportion of temperature readings which were > 27ºC in the data set showed that the percentage of burrows which had temperatures > 27ºC were significantly different for each burrow type ($F_{(5,54)} = 7.4102$ $p < 0.0001$) (Figure 4-7). The percentages of recorded temperatures above UCT for each burrow type were: artificial 11.2%, artificial with no holes 7.9%, artificial with vegetation cover (Igloo) 5.1%, grass 1.7%, sand 4.1%, and vine 3.5%.

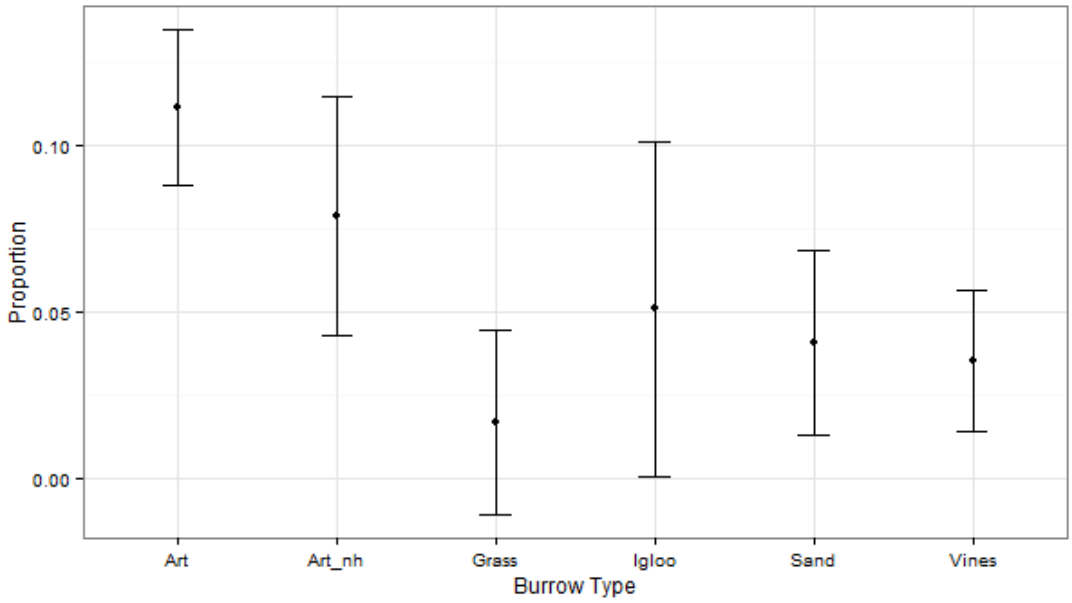


Figure 4-7 *Temperatures >27ºC for all burrow types. Artificial burrows maintain a temperature >27ºC for around 0.11 proportion of the total time, whilst grass burrows maintained a temperature of >27ºC for about 0.02 of the total time.*

Most of the temperatures > 27ºC were in the range of 27 - 30ºC (46.8%) (Table 4-6). A few temperature readings > 42^0C (3.3%) occurred in March. These very high temperatures were only found in the artificial and sand burrows.

Table 4-5 *Percentage time of temperatures > 27ºC for each little penguin burrow type. Most temperatures > 27ºC were within the range 27 – 32ºC. Artificial burrows had the greatest proportion of high temperatures; artificial burrows with vegetation covering (Igloos) and grass burrows had the lowest proportion.*

	Types of Burrows						
Temperatures >27ºC (ºC)	**Artificial**	**Artifical_nh**	**Grass**	**Igloo**	**Sand**	**Vines**	**Total % for proportion of temp >27ºC**
27-31.99	26.39%	11.27%	4.55%	3.47%	6.64%	15.01%	67.32%
32-36.99	14.02%	2.70%	0.42%	1.06%	2.39%	2.72%	23.32%
37-41.99	4.44%	0.10%	0.00%	0.00%	1.20%	0.10%	5.83%
42-46.99	1.29%	0.00%	0.00%	0.00%	0.77%	0.00%	2.06%
47-51.99	0.31%	0.00%	0.00%	0.00%	0.79%	0.00%	1.10%
52-56.99	0.00%	0.00%	0.00%	0.00%	0.33%	0.00%	0.33%
57-61.99	0.00%	0.00%	0.00%	0.00%	0.04%	0.00%	0.04%
Total %	**46.45%**	**14.06%**	**4.98%**	**4.53%**	**12.15%**	**17.82%**	**100.00%**

4.5 Discussion

Grass burrows had a mean temperature of 17.18ºC ± 1.06SE and mean relative humidity of 85.2%. At higher colony temperatures, grass burrow temperatures remained cooler than other burrow types, indicating that grass has good insulative properties. Sand burrows had a mean temperature of 18.6ºC ± 1.26SE and had similar properties to grass burrows as colony temperatures increased. However, while sand also appears to be a good insulator, the lack of ventilation leads to relative humidities greater than 90%, almost saturation point. Artificial burrows with no ventilation holes had a mean burrow temperature of 19.76ºC ± 1.82SE and relative humidity of 75.7%; the gradient (T_i - T_o) showed no pattern and burrow temperatures were more frequently warmer than the colony temperature. All nests had a buffering effect on the burrow temperatures and were cooler than the colony air temperature during the heat of the day. However, as concrete has a higher thermal capacity than sand, the temperatures of artificial burrows tended to be higher at night than the sand burrows which released heat back into the air more quickly.

Burrow types had a varying effect on burrow microclimate. Compared to natural burrows, artificial burrows maintained higher temperatures and lower relative humidities, though the values suggested that the conditions generally remained appropriate for breeding. Artificial burrow temperatures tracked the colony temperatures, whereas grass burrows did not and appeared insulated from the colony temperature. Artificial burrows reached the UCT (27ºC) more often than other burrow types. This may have implications for the breeding success of little penguins.

4.5.1 Limitations of the study

A limitation of this study was the unbalanced experimental design. Some penguin burrow types did not occur in all locations requiring consideration of the location of the colony in the analyses. The results of Model 1 demonstrate that the colony factor might have had some influence on burrow temperature but it did not have a major role in differentiating the temperatures that occurred among the burrow types.

Since monitoring of burrows only occurred fortnightly, it was not possible to assess the effect of the presence of penguins on burrow microclimate. It was also assumed that each burrow had an equal chance of a visit by a penguin, or the rabbits and bandicoots that live within the colonies. The breeding season was very poor in these colonies during 2011 - 2012; few penguins were present in the colonies during the survey time and burrows were largely unoccupied. Finally, some of the high temperatures recorded during the survey may be related to the orientation of the burrows which resulted in the sun's radiation directly striking the iButton logger in the burrow. Similarly, some of the maximum temperatures recorded by the iButton

loggers recording ambient air temperature in the colony may also have been affected by the change in the angle of the sun during the duration of the study.

4.5.2 Microclimate as a function of burrow type

The most suitable conditions for the birds almost certainly combine temperature and relative humidity, since evaporative cooling is crucial for thermoregulation (Weathers 1981). Unlike other birds, penguins have dense feathers. This makes them highly adapted to aquatic environments but results in a reduced capacity for evaporative heat loss (Stahel & Nicol 1982; Baudinette *et al.* 1986).

Temperature measured in burrows once per day in different locations, comprising caves, under bushes and two types of nest boxes on Penguin Island, Western Australia revealed no differences between colony temperature and the nests (Klomp *et al.* 1991). Conversely, hourly readings over a period of 37 days, also on Penguin Island, showed that temperatures in nest boxes were higher than in the surrounding shrubby vegetation and in summer reached higher than 40^{o}C in the nest boxes in the hottest parts of the day (Ropert-Coudert *et al.* 2004). Soil burrow temperatures were generally lower than the little penguin colony temperature on Phillip Island, Victoria (Horne 2010). Different data loggers and field techniques may account for some of these differences, in addition to differing abiotic and biotic factors within the contrasting colonies.

Artificial burrows maintained higher temperature and lower relative humidity than other burrow types. This may enable more effective thermoregulation by the birds than sand burrows, which also have high temperature but also high relative humidity. However, high relative humidity benefits incubation as reduced water loss from the egg enhances its chances of survival (Grant 1982; Deeming 2011). Relative humidity is an important aspect of other types of nest structures. Deeming (2011) and references therein found that many bird species regulate water loss from their incubating eggs by modifying nest structure. Thick cup shaped nests with walls tend to have higher relative humidity than scrape-type nests, which are more open to the environment (Ar & Sidis 2002). Burrows with a more open than closed structure also have lower relative humidity.

While incubating birds are unable to control relative humidity, their continuous presence in the burrow may lead to an increase above the ambient levels (Deeming 2011and references therein). Choosing and building appropriate nest-sites at the right time of year allows birds to influence egg mass loss by maximising relative humidity (Deeming 2011). For the same reason, Palestine sunbirds (*Nectainia asea*) position their nests to avoid excessive insolation (Sidis *et al.* 1994). The orientation of openings of nest boxes is an important determinant of their microclimate as has been found for tree swallows (*Tachycineta bicolor*) (Ardia *et al.* 2006) and American kestrels *(Falco sparverius)* (Butler *et al.* 2009). Nest box orientation resulting in lower temperatures and higher relative humidities has led to higher breeding success in barn owls (*Tyto*

alba) (Charter *et al.* 2010). For similar reasons, tall vegetation is associated with greater chick productivity than is low vegetation for lesser black-backed gulls (*Larus fuscus*) (Kim & Monaghan 2005); and Kelp gulls (*L. dominicanus)* show a strong preference for covered nest-sites as these are associated with relatively high reproductive success (Yorio *et al.* 1995). The use of covered nest-sites by little penguins indicates that penguins seek a microclimate that reduces the effect of intense solar radiation (Figure 4-6) and provides a fairly stable environment.

Wet conditions and wind lead to rapid cooling of eggs that can affect incubation energetics and consequently reproductive strategies (Hilton *et al.* 2004). Whilst increased ventilation reduced nest-site temperatures, for example in the artificial burrows, this was associated with mean lower relative humidity, which would increase evaporative rates from birds and eggs (Calder & King 1974). The degree to which this takes place could have a significant impact on the survival of eggs, chicks and attendant adults present in the burrows. Little penguins used a variety of nests and burrows. This study showed that there were significant differences between the heating and cooling characteristics of these different types of burrows over a 24-hour period. (Figure 4-4). However, the propensity for all burrow types to be occupied suggests that little penguins are able to cope with the variation in microclimate provided by the burrow types and that all provide a suitable nest-site. It is still possible that the microclimate in some burrow types is more favourable in terms of reducing the metabolic costs associated with thermoregulation, and consequently on the survival of incubating adults and chicks during the breeding season (Baudinette *et al.* 1986) with implications for chick productivity (Chapter 5).

4.5.3 The impact of burrows reaching the Upper Critical Temperature

Little penguin chicks occupy burrows for 8 - 10 weeks, moulting birds for15 - 21 days and adult birds during incubation or guard stage for up to 2 days. Chicks are more likely to experience higher burrow temperatures than adult birds during moulting as this usually takes place in late summer when temperatures are lower. Penguins are poor at coping with heat stress and small chicks are unable to thermoregulate in the first few days after hatching (Erasmus & Smith 1974).The UCT of 27ºC was reached more often in the artificial burrows. If this occurred over prolonged periods, the birds would be vulnerable to heat stress; increased panting has been recorded at temperatures higher than 27ºC (Stahel & Nicol 1988). In other penguin species, eggs have been deserted when birds have sought escape from high burrow temperatures (Boersma 1975; La Cock 1988).

Most observational studies of heat stress in the field have revealed that short periods of heat stress and elevated body temperature can occur in Galapagos (Boersma 1975), yellow eyed (Seddon & Davis 1989) and Humboldt (Simeone *et al.* 2004) penguins. However, the frequency of heat stress events has not been measured for any extended period. In Halifax, Namibia in 2000, within 2 hours of temperatures exceeding 37ºC, heat stress led to mass mortality of African

penguin eggs and chicks (Kemper *et al.* 2007). In 1990, adult mortality of penguins at Phillip Island due to heat stress accounted for ~0.2% of the recorded deaths (Dann 1992). Other occupants of burrows such as parasites are also thought to benefit from warmer conditions, as increasing temperatures create more favoured conditions for their multiplication (Goodenough & Stallwood 2012); temperatures higher than 25^{o}C are considered particularly favourable (Dawson *et al.* 2005). High relative humidity in nests has also been linked to higher presence of microbial parasites (Hubalek *et al.* 1973).

The IPCC low emissions scenario predicts a mean temperature rise of 1.6^{o}C in Tasmania, which would mean higher temperatures in the early part of the breeding season; under a high emissions scenario the mean temperature rise would be 2.9^{o}C over the 21st century (Grose *et al.* 2010). The frequency of temperatures higher than 27^{0}C has the potential to increase the risk of heat stress in penguins and their chicks. Even though studies have shown that early breeding leads to higher breeding success (Reilly & Cullen 1981; Chiaradia & Kerry 1999; Sidhu *et al.* 2012), it remains unknown whether this would still be the case under the above climate-change scenarios.

A study of little penguins in three locations in Australia showed that the most northern population on Penguin Island, Western Australia experienced burrow temperatures in burrows higher than 30^{o}C more frequently than did the population on Phillip Island, Victoria (Horne 2010). In this study on the North West Coast of Tasmania, burrows reached higher than 27^{o}C for a small proportion of the time. Increasing sea surface temperature (SST) and temperatures over land are likely to have competing effects on the success of little penguins in their colonies. A 40-year study on Phillip Island, Victoria, demonstrated a trend towards later mean laying dates (~0.65 days per year) (Cullen *et al.* 2009). A consequence of this is that chick rearing is taking place later, and in the warmer parts of the summer. If this is also occurring in Tasmania, and if temperatures increase as predicted, eggs, chicks and adults are likely to experience difficulties during the breeding season. Conversely, increased SST trends indicate little penguins breeding earlier in the season which might be a positive outcome for the penguins (Chambers 2004; Cullen *et al.* 2009; Chambers *et al.* 2011).

4.5.4 Implication for use of artificial burrows for conservation and management

The microclimatic characteristics of natural burrows were not reflected in artificial burrows. This is important when considering the introduction of artificial nest-sites into a habitat for management and conservation. Artificial burrows are often a feature of seabird colonies. Their success has been demonstrated by improved breeding success, for example, in African penguins (Kemper *et al.* 2007; Sherley *et al.* 2012), little penguins elsewhere in Australia and New Zealand (Perriman & Steen 2000) and Humboldt penguins in Peru and Chile (Paredes & Zavalaga 2001). Artificial burrows may also be more effective than natural burrows in preventing access by predators because of their design and construction, adding to their success for breeding. A related

approach, the introduction of artificial nest boxes has also been used successfully for establishing new colonies of Gould's petrel on Boondelbah Island (Priddel *et al.* 2006). The success of artificial burrows demonstrates that despite the potential for adverse microclimates, these burrow types are currently an effective conservation tool.

As a comparison of different artificial burrow materials and designs is required to ascertain how the most suitable microclimatic conditions can be created. The impact of these nest-sites on chick production is explored in Chapter 5.

CHAPTER 5

Nest site selection of the little penguin (*Eudyptula minor*)

5 Nest-site selection of the little penguin (*Eudyptula minor*)

5.1 Abstract

A variety of materials are used by little penguins for burrows. These include artificial material that can provide an alternative burrow type in degraded habitats. Colonies of little penguins found along the North West Coast of Tasmania live in a heavily modified habitat where artificial burrows have supplemented the natural nesting habitat. Chick production, defined as the ratio of the number of chicks produced to the total number of active burrows in each burrow type was estimated by monitoring four types of penguin burrows (grass, vine, sand and artificial) over three breeding seasons; 2010 - 2011, 2011- 2012 and 2012 – 2013. Chick production was significantly higher in artificial compared to natural burrows. Vine burrows, whilst the most densely spaced, had higher chick production in comparison to grass and sand burrows but the difference was not significant. This study confirmed that artificial burrows that are widely used in conservation and management areas where habitat has been degraded or modified, can provide successful breeding sites for little penguins.

5.2 Introduction

Investment in reproduction must outweigh the costs in a way that results in the long term maximisation of an individual's reproductive value; this is defined as the mean amount of future reproductive success of an individual in a population (Williams 1966). Many factors contribute to this value, and for birds includes the selection of a suitable nest-site (Cody 1985; Clark & Shutler 1999). Choice of nest-site influences, amongst other things, whether eggs and sedentary young may be discovered by predators and parasites. This suggests that over time, nest-site choice evolves to maximise fitness for the species (Chalfoun & Schmidt 2012). Habitat choice in a heterogeneous habitat is a consequence of natural selection having favoured individuals that recognise, are attracted to, and preferentially settle in, the best available habitat (Fretwell & Lucas 1970). It is also important to note that while species can adapt to different habitats, they may also influence their habitat (Southwood 1977).

Burrowing seabirds breed in a diversity of habitats, either under vegetation on the surface or underground. Burrows provide a suitable microclimate for chick-rearing and protection from predators, and their quality influences the survival of chicks and adults (Thompson & Furness 1991). For example, the breeding success of Manx shearwaters (*Puffinus puffinus*) on the island of Rhum was affected by the amount of rain and subsequent flooding of burrows, particularly during incubation (Thompson & Furness 1991; Kaiser & Forbes 1992). Nest-site characteristics such as lateral and overhead cover, good drainage and visibility have been found to affect nest quality in European shags *(Phalacrocrax aristotelis)* (Velando & Freire 2003). Little terns *(Sternula albifrons)* avoided placing their nests in vegetated areas and selected locations towards

the landward part of sandy beaches to avoid flooding; however these behaviours did not seem to affect nesting success (Medeiros *et al.* 2012). High quality nesting habitat, generally under vegetation, was one of the factors found to influence fledgling numbers of little penguins on Lion Island, New South Wales, Australia (Knight & Rogers 2004). Nesting success of African penguins was influenced by burrow density with burrow collapse occurring at high densities (Seddon & Vanheezik 1991); covered nests were more successful than open nests (Kemper *et al.* 2007).

The location and size of little penguin colonies is limited by available nesting habitat and the location of marine food resources (Dann & Norman 2006). Colonies across southern Australia (and New Zealand) are exposed to different environmental conditions, and these result in differences in breeding success among the colonies on a regional scale. For example, sea surface temperature and oceanographic currents affect the timing and breeding success of little penguins because of changes in availability of food sources for the chicks (Chambers 2004; Cullen *et al.* 2009; Cannell *et al.* 2012).

Across their geographic distribution, the life cycle of little penguins is adapted to the prevailing environmental cycle. This maximises the availability of food during the breeding season and results in the commencement of egg laying in Western Australia in July to as late as October in the eastern states. In general, eggs are incubated for 35 days (Chiaradia & Kerry 1999) followed by a guard phase of about 14 days and post guard phase of approximately four weeks. The earlier in the season that eggs are laid, the greater the chances of survival of birds in their first year at sea (Reilly & Cullen 1981; Sidhu *et al.* 2012). While these rates of survival may in part be a consequence of oceanographic conditions, they may also be related to microclimatic aspects of the burrow environment (Chapter4). Good burrow quality can therefore contribute to successful breeding.

In many areas of the world artificial nest-sites, which supplement natural types of sites, have been used successfully as a management tool in the conservation of seabirds. The habitat of little penguins on the North-West Coast of Tasmania has been modified. In some nest-site areas this consists of revegetated landfill containing old road and building materials (Parsonage Point colony). Habitat vegetation overall is a mixture of native and exotic species. Most of the colonies are restricted to coastal areas due to the presence of a fence, which prevents fatalities on adjacent roads, and the train track. Fences have also been used to contain penguins and prevent them spreading under urban dwellings (Parsonage Point, and Doctor's Rocks colonies). As a result, artificial burrows have been utilized to offset the loss of habitat in these peri-urban Tasmanian colonies, but little is known of the chick production and breeding success of their users. The characteristics of the types of burrows used by penguins in North West Tasmania were explored in Chapters 3 and 4.The influence of burrow type on nest-site selection and chick production of little penguins among the study colonies is examined in this chapter.

The hypotheses tested in this study were:

H_0; there is no difference in chick production among burrow types.

H_0; the number of chicks produced in artificial burrows is less than in other burrows

5.3 Methods

5.3.1 Study Sites

Two little penguin colonies (Doctor's Rocks and Parsonage Point) on the North West Coast of Tasmania were used as the study sites (Figure. 5.1).

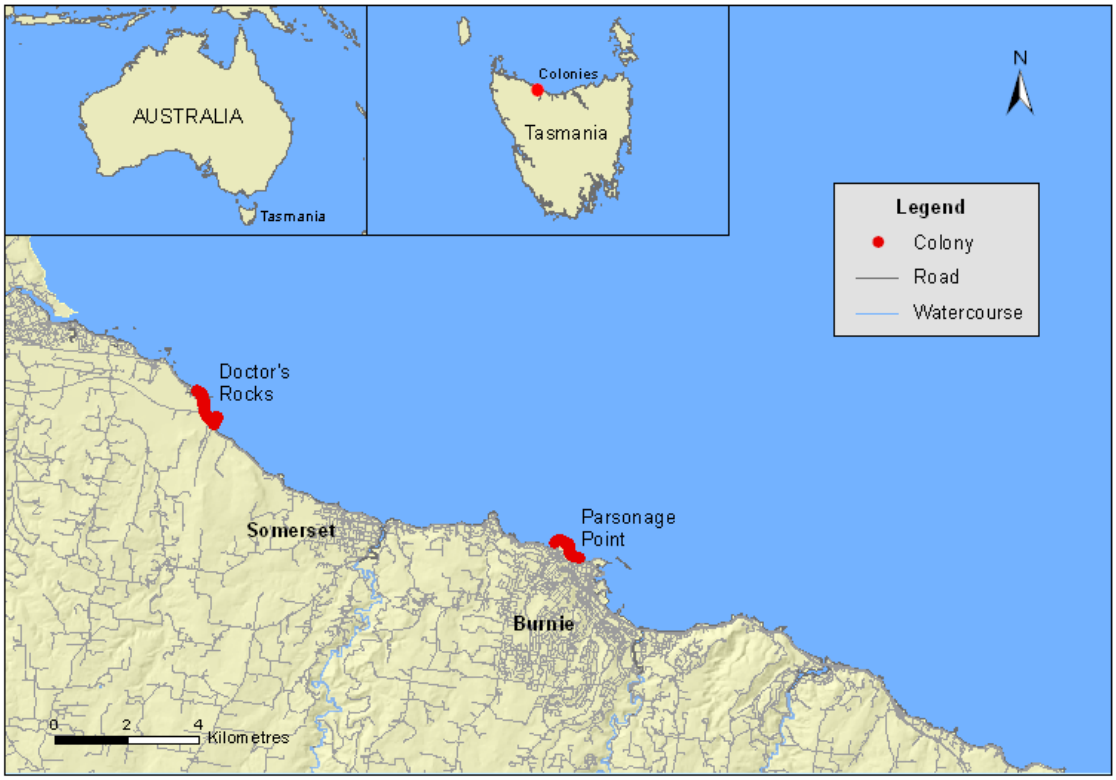


Figure 5-1 *The location of two little penguin colonies on the North West Coast of Tasmania, Australia.*

The Doctor's Rocks colony (-41.00ºS 145.77ºE) 12km west of Burnie, is about 1km in length and composed of a variety of vegetation ranging from shrubs (mostly *Correa* sp., tea tree sp.) to tussocks (*Poa* sp.) and vines (*Tetragonia* sp.). It contains vegetation (grass and vines), substrate (mostly sand) and 34 artificial burrows, which are in the form of concrete igloos, and were placed in the colony in the early 2000s to replace habitat lost by the erection of a fence (Figure 5- 2).

The second colony is 12 km away, at Parsonage Point **(**-41.04 ºS 145.89 ºE), and is a headland consisting of old landfill made of building material that has been revegetated; the vegetation is mostly grasses and shrubs with very little substrate for burrows. Penguins have bred in this region since at least the 1960s. The colony was fenced in 2002 to prevent road and rail

fatalities, blocking access to other areas previously used for nesting by penguins. To offset the loss of habitat, 154 artificial burrows, also concrete igloos, were added to the colony and have been used successfully for breeding for over 10 years (Figure 5-2a).

Four main types of burrows were used at these two sites and they were classified as either sand, grass, vines or artificial (Table 5-1 and Figure 5-2). This allowed *nano*-scale comparison of chick production among the burrow types. The distribution of burrow types at Doctor's Rocks (Figure 5-3) and Parsonage Point (Figure 5-4) show that the former contains mostly natural burrows whilst the latter contain mostly artificial burrows.

Table 5-1 *Summary of burrow types and their locations in this study (See Chapter 2)*

Type of burrow Below -(B) or Above-ground (A)	**Definition**	**Colony**	**Sample size: Number of burrows monitored over the 3 years**
Sand (B) Including rock(B)	No vegetation used in the construction of the burrow.	Doctor's Rocks Parsonage Point	31-35 3-4
Grass (A)*	Long, strappy blades of varying thicknesses that overlap each other.	Doctor's Rocks	4-16
Vines (A)*	Climbing, twining, winding or sprawling plants, usually with a woody stem.	Doctor's Rocks Parsonage Point	2-17 1-2
Artificial (A)	Artificial structures that are made of concrete and look like igloos in most cases.	Doctor's Rocks Parsonage Point	5-8 29-66

* See Appendix 1 for full species list

Burrows were haphazardly selected, and when chosen burrows were too deep to observe the contents, then the next closest one was selected. Burrows were monitored with a burrow camera, or in short burrows by eye, on a fortnightly basis at both colonies over three seasons, although for logistical reasons sometimes only monthly readings were possible. The contents of each burrow (empty, egg present, the number of chicks) were recorded on each visit.

Figure 5-2 *Types of burrows a) Artificial, b) Grass, c) Vine, d) Sand. Burrows found in both Parsonage Point and Doctor's Rocks colonies*

The number of occupied burrows as a ratio of the total number of burrows referred to as the *occupancy rate*, was measured. The measure of reproductive success used in this study was the number of chicks produced / total burrows in each burrow type. This is referred to subsequently as the *chick production*.

5.3.2 The models

A generalised linear mixed model (GLMM) with logit link and binomial response was used to investigate the influence of burrow types on *chick production* of the little penguins over three yearly periods. The R software package *nlme* was used (R Core team 2013) where the response variable was presence of chicks in the active burrows with fixed terms being the burrow type (*btype*) and year (*year*). Colony was used as a random term. Year was a fixed term as there was inter annual variability in breeding success and the sample size varied among the years. A *post hoc* contrast matrix was then used to test the significance of the burrow types using the R software package *multcomp* (R Core team 2013).

A second GLMM was carried out where the response variable was the number of chicks in the active burrows with fixed terms being the burrow type (*btype)* and year (*year*) with colony as the random term.

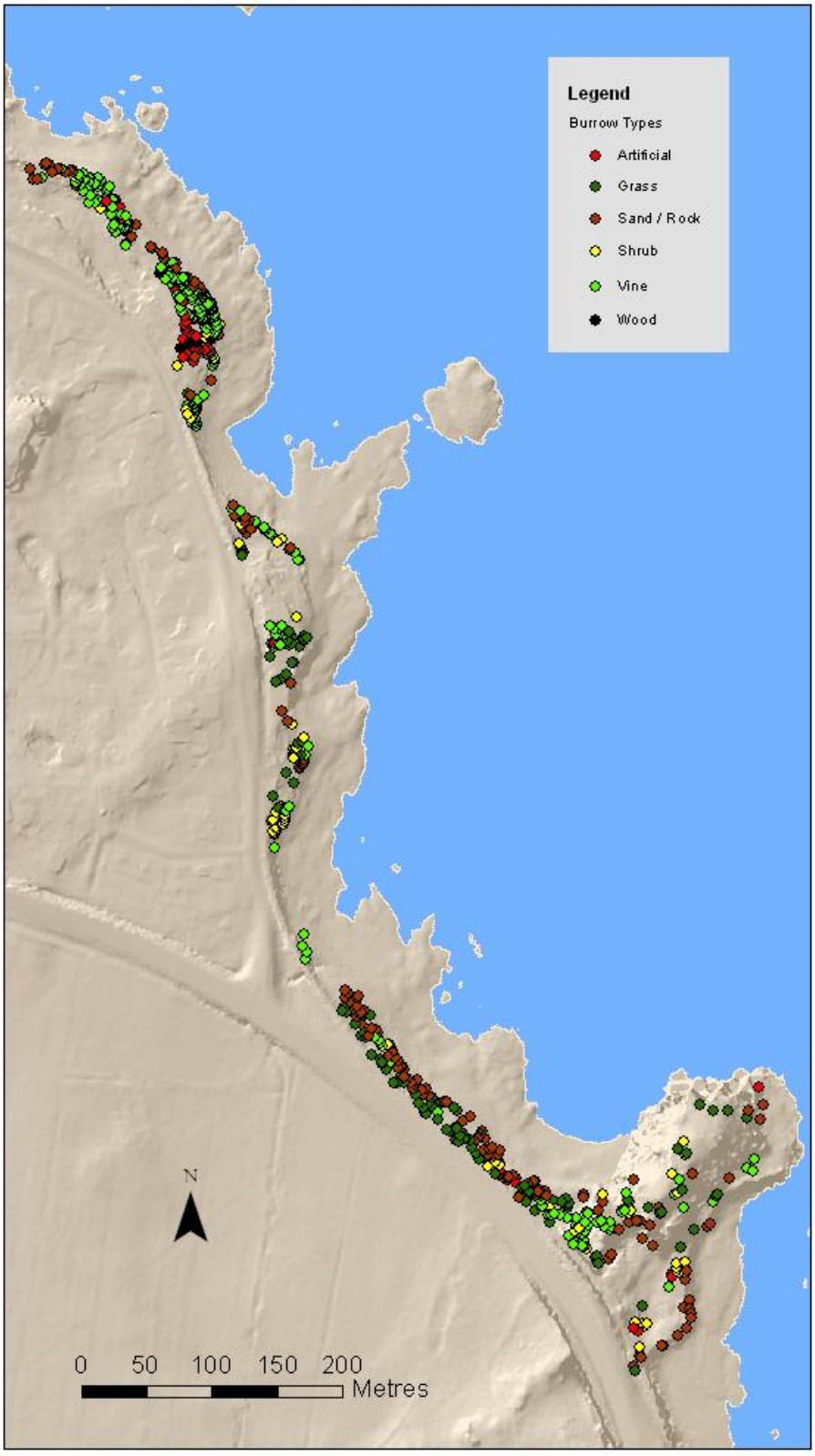


Figure 5-3 *Distribution of the different burrow types in Doctor's Rocks colony. Burrows were categorised as one of six types. Artificial, vine, sand, rock, shrubs, wood and grass burrows were identified in monitoring in this study of the breeding cycle. However, only the four main ones; artifical, grass, vine and sand were used in this study.*

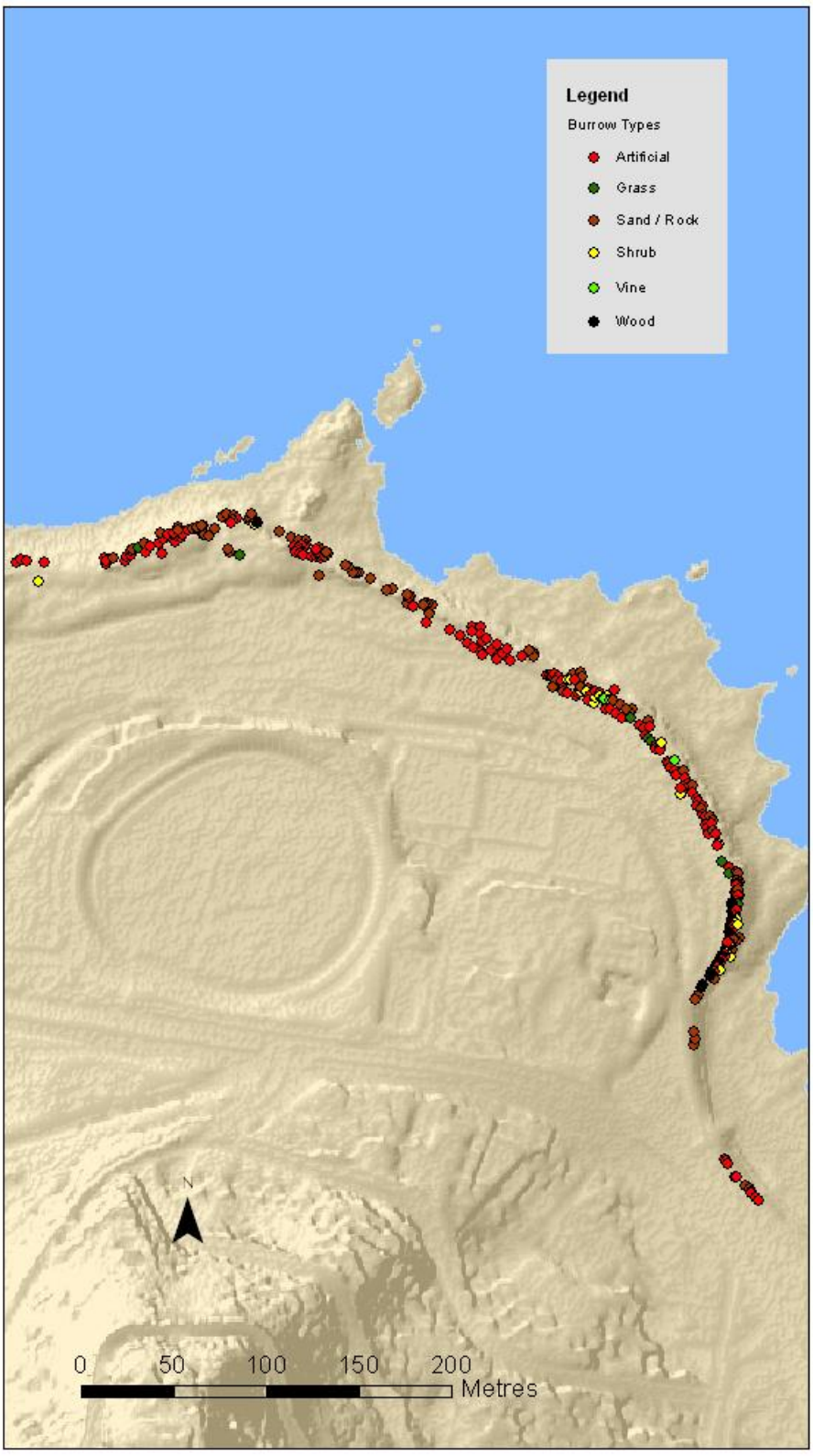


Figure 5-4 *Distribution of the different burrow types in Parsonage Point colony. Burrows were categorised as one of six types. Artificial, vine, sand and grass burrows were used in monitoring in this study of the breeding cycle.*

5.4 Results

5.4.1 Inter annual differences

Table 5-2 *Summary of inter annual breeding characteristics for comparison among colonies.*

Colony	**Parsonage Point**			**Doctor's Rocks**		
	2010 /11	**2011/12**	**2012/13**	**2010 /11**	**2011/12**	**2012/13**
Total no. of burrows sampled (n)	30	47	71	42	82	79
No. occupied burrows / total (Occupancy rate)	0.90	0.94	0.73	0.76	0.56	0.58
Number of chicks / total number of active burrows (Chick production rate)	**1.30**	**1.70**	**0.94**	**0.95**	**0.83**	**0.46**

Both the proportion of burrows occupied and the proportion with chicks varied annually in both colonies (Table 5-2). The occupancy rate was higher at the Parsonage Point colony in comparison to the Doctor's Rocks colony, with the highest value obtained in 2011/12 at Parsonage Point (0.94 burrows / total). Interestingly, the chick production rate, whilst fluctuating among the years, was also always higher at Parsonage Point than Doctor's Rocks. This may reflect the types of burrow used at Parsonage Point in comparison to Doctor's Rocks (Figure 5-2 and Figures 5-3, 5-4).

5.4.2 Chick production as related to burrow type and year

The GLMM indicates that the best model, AIC 400.32 (Table 5.3), was:

Chick production ~ year + btype +location

There was no interaction between the year and burrow type, AIC 409.14 (Table 5-3), which shows that burrow effect was constant among years. Further, the presence of chicks was higher in artificial burrows than in other burrow types (Figure 5-5). The presence of chicks was higher in vine burrows than in other natural burrows, but this was not significant (Table 5-4).

Table 5-3 *Summary of generalised linear mixed-effect model (GLMM) comparisons with Chick present as the response variable (Year = three years of monitoring, btype= type of burrow) and Location (colony) as a random factor. The best model is presented in bold.*

Candidate models	np	AIC	ΔAIC	wAIC
C~ year+btype	**3**	**400.3298**	**0.0000**	**0.9163**
C~ year	2	405.4302	5.100414	0.0715
C~ btype*year	3	409.1438	8.813991	0.0111
C~btype	2	414.1931	13.863286	0.0008
C~ null	1	419.7376	19.407781	0.0001

np: number of parameters , AIC: Akaike's Information Criterion, **Δ**AIC: difference in AIC from that of the best fitting model, *w*AIC: AIC weight

The fitted values for all three seasons also show a consistency in pattern of chick production across burrow types, with the highest chick production obtained in artificial burrows, and the lowest in grass burrows (Figure 5.5).

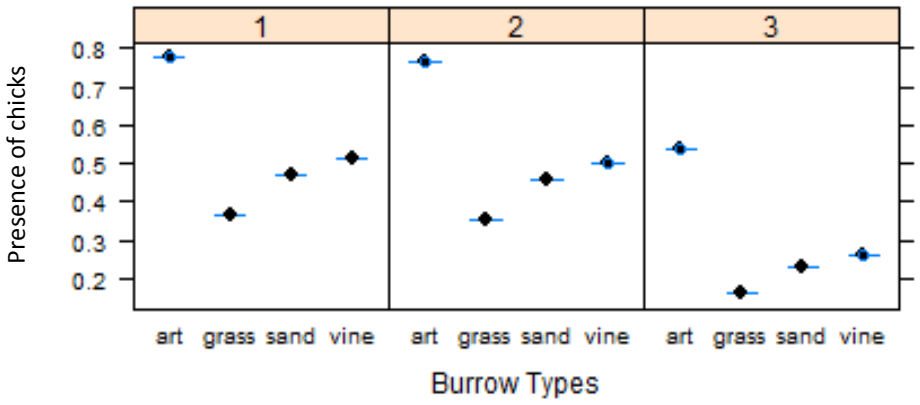


Figure 5-5 *Fitted values (presence of chicks) plotted against burrow types (art= artificial burrows, grass, sand and vine burrow across all 3 years (1=2010/11, 2= 2011/12 and 3 = 2012/2013 seasons). The result is a consistent pattern where artificial burrows have a higher chick production compared to the natural burrows in all three seasons. Within the natural burrows, the vine category is always slightly better than the other categories.*

A *post hoc* contrast matrix confirms chick production in artificial burrows is significantly higher than those in grass, sand ($p<0.0001$) and vine burrows ($p<0.05$) (Table 5-4), but chick production in vine burrows did not differ significantly from the other natural types of burrows.

Table 5-4 *Contrast matrix showing P-values from simultaneous tests for general linear hypotheses (glht) multiple comparisons of means: Post hoc Tukey Contrasts across all burrows.*

	Artificial	**Grass**	**Sand**	**Vine**
Artificial	-			
Grass	<0.001**	-		
Sand	<0.001**	0.846	-	
Vine	0.024*	0.777	0.997	-

5.4.3 Number of chicks per burrow type

The GLMM indicates that the best model, AIC 835.09 (Table 5.5), was:

Chick number~ year

There was no interaction between the year and burrow type, AIC 848.34 (Table 5-5), which shows that burrow effect was constant among years. Further analysis of the burrow types shows that the numbers of chicks were higher in artificial burrows than in other burrow types (Figure 5-6).

Table 5-5 *Summary of generalised linear mixed-effect model (GLMM) comparisons with Chick numbers as response variable (Year = three years of monitoring, btype= type of burrow) and Location (colony) as a random factor. The best model is presented in bold.*

Candidate models	**np**	**AIC**	**ΔAIC**	**wAIC**
C~ year	**2**	**835.0864**	**0.0000**	**0.8107**
C~ year+ btype	3	838.1759	3.089449	0.1729
C~null	1	843.5172	8.430761	0.0111
C~btype	2	846.1177	11.031247	0.0033
C~btype*year	3	848.3367	13.250248	0.0011

np: number of parameters, AIC: Akaike's information Criterion, ΔAIC: difference in AIC fomr that of best fitting model, wAIC: AIC weight

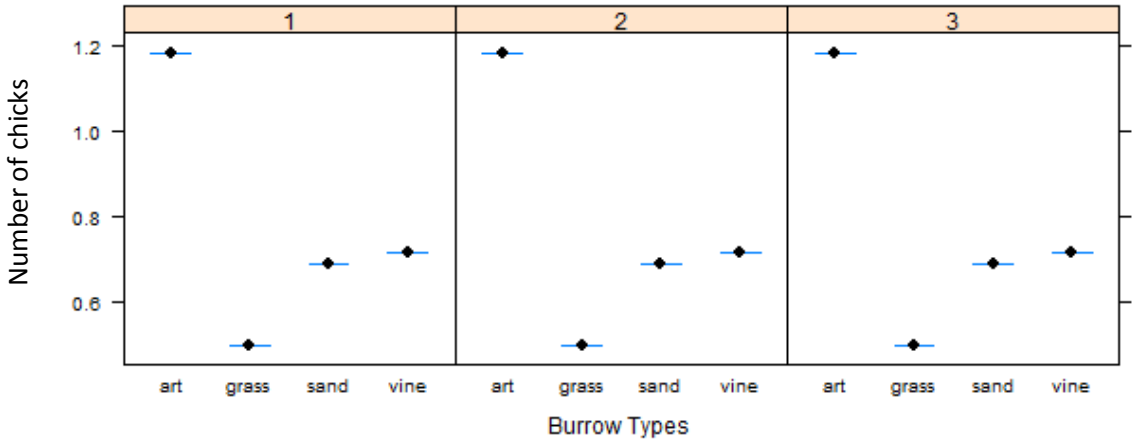


Figure 5-6 *Fitted values (number of little penguin chicks) plotted against burrow types (art= artificial burrows, grass, sand and vine burrow across all 3 years (1=2010/11, 2= 2011/12 and 3 = 2012/2013 seasons). The result is a consistent pattern where artificial burrows have a higher number of chicks compared to the natural burrows in all three seasons. Within the natural burrows, the number of chicks is always lower in the grassburrows compared to the other categories in all three years.*

5.5 Discussion

Burrow type clearly has an effect on breeding success of the penguins; the higher production of chicks at Parsonage Point (Table 5-2) is likely to be due to the much larger number of artificial burrows that are present there than at Doctor's Rocks (Figure 5-2 and Figure 5-3). Artificial burrows were found to be significantly different from other burrow types, independent of any site effect (Table 5-4), producing more chicks in each of the three years (Figure 5-5) and a higher number of chicks per burrow (Figure 5-6).

Other studies that have compared breeding success in artificial burrows to that in natural burrows have shown similar results. Higher breeding success was seen in little penguins that bred in nest boxes in Otago, New Zealand compared to natural nests, except when heavily predated by rats (Johannesen *et al.* 2002).

Factors that affect the breeding success of a nest-site fall into two categories: 1) physical and spatial factors: nest structure, microclimate, location in the landscape, and attributes such as slope, aspect, dryness, solar radiation and density; and 2) biological factors: the age of the breeding birds, body condition, interaction with conspecifics, predation and prey availability.

5.5.1 Physical factors

Slope, aspect, incident solar radiation and dryness determine where the nest-sites are located within a colony (Chapter 3). The microclimate of the nest-sites is affected by the material from which they are constructed, and this may affect the energy costs of thermoregulation by the chicks (Stahel & Nicol 1982). Artificial burrows were approximately 2.2ºC warmer than other burrows (Chapter 4), but within the range that allowed chicks to be raised successfully.

Nearest neighbour distances were shorter among vine burrows (Chapter 2), suggesting that they are preferentially selected by breeding birds, because of an expectation of higher breeding performance than other natural burrow types (Figure 5-4); however, the *post hoc* comparison across all burrows (Table 5-4) indicates no significant difference in chick production across natural burrow types. Consequently, the density of vine burrows does not appear to be linked to chick productivity. Higher nest density can be an indication of good habitat but there may be a threshold where, if the density increases beyond a certain point, habitat quality decreases (Van Horne 1983). This may result in a sink habitat, whereby chick productivity declines. Local colonies may have high densities due to local depletion of prey, but may also increase disease transmission and predation.

The philopatric nature of penguins may also result in a depressed breeding rate if the density of burrows increases over time. An inverse relationship between nest density and breeding performance has been demonstrated in glaucous-winged gulls (*Larus glaucescens*) (Hunt & Hunt 1976), African penguins (*Spheniscus demersus*) (Sherley *et al.* 2014) and magellanic penguins (Stokes & Boersma 2000). However, the reasons for the variation in breeding success may be competition among conspecifics for nest-sites (magellanic penguins), or the increased competition for prey (glaucous-winged gull) that then influences the breeding success as a result of the high nest density. Another possible factor that may result in decreasing chick production with increased density of nests may be a higher risk of parasites and disease. For instance the ectoparasitic argasid tick (*Ornithodorus amblus*) was found to cause desertion of nests of the three main Peruvian guano birds: the guano cormorant (*Phalacrocorax bougainvillii*), the Peruvian booby (*Sula variegate*) and the Peruvian brown pelican (*Pelecanus occidentalis thagus*) when nest density was high (Duffy 1983). However, warmer climatic factors may play more of a role in the increased prevalence of the ectoparasite.

5.5.2 Biological and social aspects

This is the first time chick production has been quantified in these colonies in North West Tasmania; the age, fecundity and other biological factors of the breeding penguins are still unknown. Although the quality of food that is fed to chicks may affect their survival (Kato *et al.* 2001; Sherley *et al.* 2013; Kowalczyk *et al.* 2014), it could be assumed that because of the

proximity of the colonies (12 km apart) the birds from Doctor's Rocks and Parsonage Point are foraging in the same area. Two little penguin colonies 70 km apart in Victoria that have overlapping foraging areas, showed segregation in the areas (Chiaradia *et al.* 2012). The lack of foraging data of the study indicates some further research is needed.

Parental age has an effect on breeding potential, with older birds being more successful (Bunce *et al.* 2005), for example thick billed murres (*Uria lomvia*) (DeForest & Gaston 1996) and Australasian gannets (*Morus serrator)* (Pyk *et al.* 2007). Age and pair-bond duration, as well as nest-site and partner fidelity (Nisbet & Dann 2009), also influence the breeding performance of little penguins. Earlier laying also results in improved breeding success in the little penguin (Agnew *et al.* 2014). The link between age and foraging success has been demonstrated for little penguins, whereby middle–aged females showed better foraging performance than young and old penguins and, consequently better chick provisioning (Zimmer *et al.* 2011).

5.5.3 Comparison of nest types and their influence on chick production

A summary of the breeding habitats and burrow types of nesting penguins found in Australia and elsewhere (Table 5-6) indicates that a variety of vegetation types and structures are used as nest-sites, depending on the characteristics of the colony. Over a wide range of locations, birds have the potential to raise chicks in a variety of nest-sites, which are generally roofed over in some way. African penguins which breed in surface nests where there is a lack of cover tend not to be very successful due to the high rate of predation (Pichegru 2013) and levels of solar radiation (Sherley *et al.* 2012). Selection of nest types by penguins appears to be based on the available material at the colony sites. Structure and sturdiness of nests may in fact be a contributing factor to the number of little penguin chicks fledged due to the better protection from climatic extremes, flooding and predation (Bull 2000).

Artificial burrows are used for many bird species as a management tool to assist in the remediation of poor, degraded sites where habitat has either been lost or modified. Artificial burrows (made of wooden boxes or fibre glass) resulted in higher reproductive success in African penguins in comparison to vegetation burrow types over a 10-year study period; fledging of the chicks was 8 - 14% higher in artificial burrows than under vegetation (Sherley *et al.* 2012). Similar results were achieved with the blue penguin (*Eudyptula minor*) at Taiaroa Head, Otago Peninsula (Perriman & Steen 2000) and at Oammaru, New Zealand (Houston 1999) where wooden nest boxes were used successfully, although in this case no non-nest box data were available for comparison. Wooden nest boxes have also been used successfully by yellow-eyed penguins *(Megadyptes antipodes)* in North Otago, New Zealand in preference to natural vegetation, especially where forest breeding areas have been lost to agriculture (Lalas *et al.* 1999). A recent study at Phillip Island examining 25 years of data indicated that survival of little penguin chicks was higher in artificial burrows in poorer years and not significantly different in good years (Sutherland *et al.* 2014).

Artificial burrows may provide better protection from predators due to their solid construction and single opening. Also, the energetic requirements of actually excavating a natural burrow compared with an artificial, pre-prepared, nest site needs to be considered. Natural burrows can collapse so can jeopardise the survival of a clutch and require the energetic costs of reconstruction elsewhere. Whilst artificial burrows present a ready shaped burrow for little penguins that reduces energy costs, some still require further excavation of the bowl into the soil where that is possible; however, they also provide opportunities for nesting in areas where the ground may be too hard and compact for making burrows. The microclimate of the burrows may also be more suitable for raising chicks (Chapter 4). Artificial burrows could be considered as higher quality nesting sites due to the higher chick production, which may be due to thermal properties, or location within the colony (Sutherland *et al.* 2014). They may also provide protection from severe weather as they tend to be of a solid construction (Braidwood *et al.* 2011). The higher chick productivity also indicates that artificial burrows are not ecological traps and suggest that they are a useful addition for conservation and management of little penguins in modified habitats.

A conceptual model is proposed (Figure 5-7) that examines the integration of factors that may have a significant role in determining the chick productivity of nest-sites. Physical characteristics are represented in the large top oval. Spatial factors include the nearest neighbour distance that determines the density of nest-sites (Chapter 2) which may influence social interactions and other density dependent factors such as the presence of parasites and diseases. Terrain values influence the properties of the nest-site such as whether it is warm, dry and on a shallow slope (Chapter 3). Location of a burrow in relation to the size and shape of a colony will also affect the propensity for predatory attack and consequently the probability that the burrow may be successful in terms of chick productivity. The microclimate of a burrow which is largely determined by the structural material of the nest will also influence chick productivity (Figure 5-6).

The success of a nest-site in terms of chick productivity also relies largely on the biological characteristics of its occupant parent birds. Are the birds good mates as parents and how many chicks can they successfully raise? The experience of older birds is associated with well-developed skills in raising young more efficiently and successfully than younger birds (Weimerskirch 1990). The availability of food has a major influence in determining when the breeding season commences and its success. In poor seasons only high quality individuals will produce chicks successfully (Oro *et al.* 2014). However, in a good year given adequate food supply, nest-site characteristics will more than likely play a role.

This study raises questions about the role of the burrow type and its associated microclimate in breeding success. A long-term study would be required to investigate biological factors such as whether “better birds” get better burrows, and whether birds return to the same

burrow or burrow type if they raised chicks to fledgling state. This would help determine the lifetime reproductive success of the different burrow types.

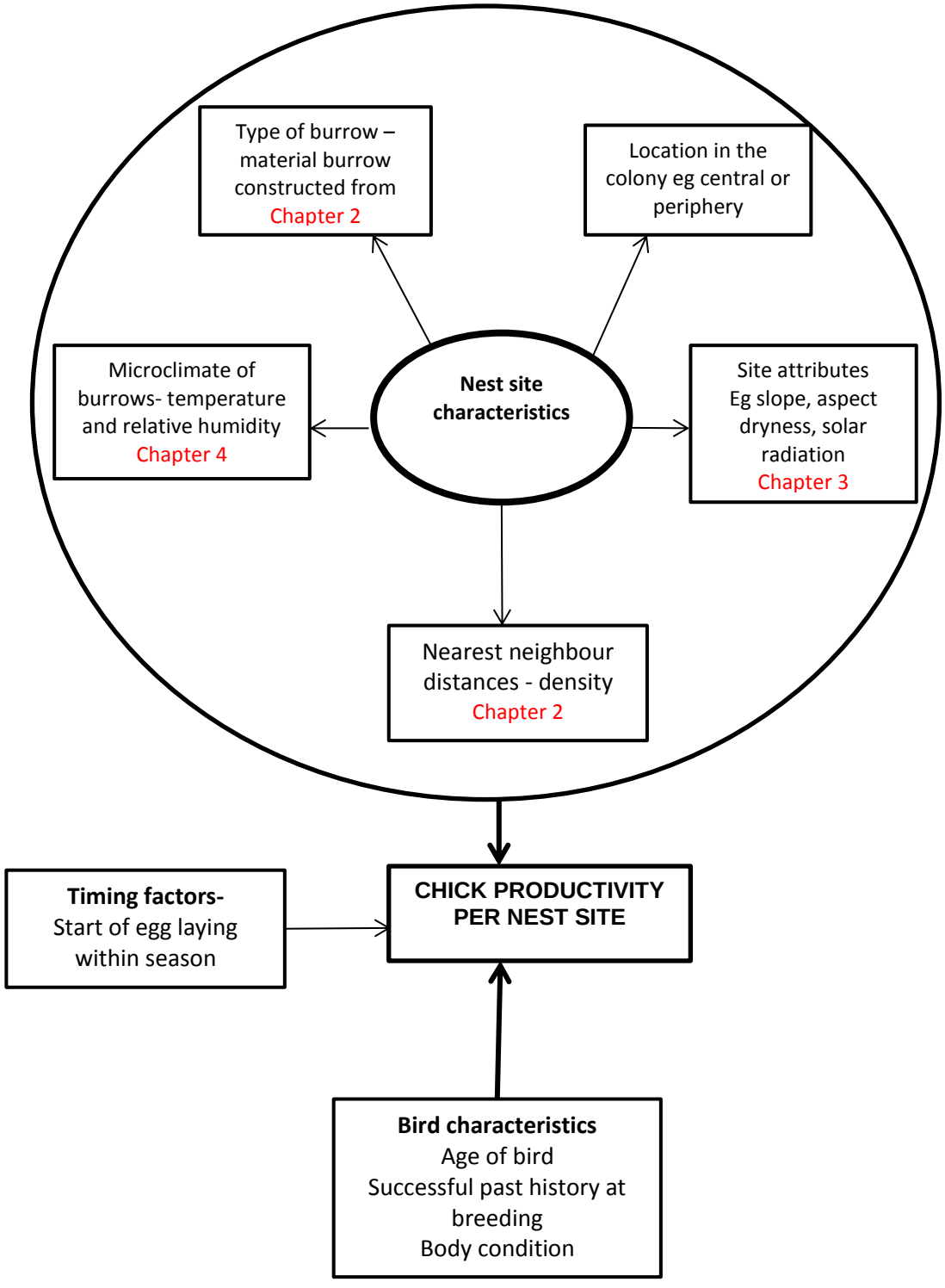


Figure 5-7 *A conceptual model that indicates factors that may affect the productivity of the nest site of a burrowing seabird (eg little penguins). Structural and spatial features of nest sites are identified in the top oval and biological factors of a species are identified in the bottom box.*

Table 5-6 *Types of burrows used by burrowing penguins in other sites. Colonies that use artificial burrows are also indicated in the table*

Colony	Source of nests / burrows	Artificial burrows	Other contributing factors	Reference
Australian colonies - Little penguin (*Eudyptula minor)*				
Penguin Island, WA	Low bushes Shrubs, rock crevices, caves	Wooden boxes	Sand too soft for burrows	(Klomp & Wooller 1991; Ropert-Coudert *et al.* 2004)
North Harbour, NSW	Rock cavities,	Wooden boxes	Limited to boulder rock platform, so no access to sandy substrate.	(Priddel *et al.* 2008)
Phillip Island, V	Soil burrows, Tussock burrows	Wooden boxes		(Dann *et al.* 1992b) (Sutherland *et al.* 2014)
Lion Island, NSW	Low woodland, Creepers, Rocks	-		(Rogers & Knight 2006)
Bowen Island , NSW	Woodland (*Banksia sp*)	-		(Fortescue 1999)
Middle Island	Tussock grass land	-		(Overeem & Wallis 2003)
Montagu Island, NSW	Kikuyu grass	-	No underground burrows	(Weerheim *et al.* 2003)
Islands adjacent to Wilson Promontory N Central Bass Strait	Tussock grass, Scrubland (*Lavatera sp)*. Coastal shrub	-		(Schumann, Dann & Arnould 2013)
North West Coast Tasmania	Sand, rocks, shrubs, vine, grass	Artificial cement burrows		(This study)
Other burrowing penguin species				
Otago, New Zealand Yellow eyed penguins *(Megadyptes antipodes)*	Old rabbit burrows, under rocks, Mingimingi *(Coprosma sp*), and other shrubs	Wooden boxes		(Lalas *et al.* 1999) (Johannesen *et al.* 2002)
South Westland, Otago,New Zealand Blue penguin (*Eudyptula minor*)	Rocks, caves, under vegetation in soil and sand	Wooden boxes		(Dann 1994; Braidwood *et al.* 2011)
Robbens Island, South Africa African penguin (*Spheniscus demersus*)		Wooden boxes, fibre moulds concrete	Removal of guano soils used for burrowing has made surface nesting the main option	(Sherley *et al.* 2012) (Lei *et al.* 2014)
Halifax Island, Namibia African penguin (*Spheniscus demersus*)	Native bush, buildings	Half plastic bins	Removal of guano soils used for burrowing has made surface nesting the main option	(Kemper *et al.* 2007)
Peru Humboldt penguin (*Sphensicus humboldti)*	Surface with mixture of stones, guano, burrows in substrate, crevices		Guano depletion has led to surface nesting	(Paredes & Zavalaga 2001)

CHAPTER 6

Location, Location, Location – but at what scale?

6 Location, Location, Location – but at what scale?

6.1 Synopsis

Habitat heterogeneity exists within a hierarchy of spatial and temporal scales, and has become an increasingly significant component of ecological studies. This approach has led to improved understanding of the ecological processes relevant to the species under study (Wiens 1989). It has confirmed what ecologists often assumed were the most important ecological processes affecting populations and communities, *i.e.* those that operate at local spatial scales (Cody 1985).

The spatial scales relevant to a burrowing seabird are its geographic range, and the locations of the colony, and its nest-site within the colony. The distribution of little penguins in Australia is delimited by a climatic envelope defined by the 20^{o}C water summer isotherm (Dann *et al.* 1996). This study has shown that little penguin colonies on the coast of Tasmania at a *meso*-scale (100s of kilometres) are regularly rather than randomly distributed or clustered, suggesting that the most influential variable at this scale could be proximity to foraging areas. At a *topo*-scale (10s of kilometres), the distribution pattern of colonies was influenced by the effects of human disturbance, which has possibly resulted in the fragmentation once larger colonies. At the *micro* scale (<10s of metres), nest-sites within colonies were largely clustered, which suggests that a particular set of variables is required for little penguins to establish nests within colonies (Chapter 2). Although a variety of burrows were used by little penguins, most clustering was associated with vine vegetation (Chapter 2).

Terrain variables (*slope, aspect, elevation, solar radiation, wetness index*) and *distance to the coas*t were used to model the location of nest-sites within the colonies (Chapter 3). Penguins select dry, northerly facing aspects with some slope (to allow digging). Burrow microclimate varied among the different burrow types and appeared to be suitable in all burrow types (Chapter 4). Burrow productivity (the number of chicks that are fledged per burrow type) appeared to be significantly higher in artificial burrows than in other types (Chapter 5).

This discussion of the findings of this study is based on four themes that embrace the factors currently considered to affect the distribution of burrowing seabirds 1) the hierarchical spatial distribution of seabirds' breeding habitat; 2) the definition of a colony; 3) the relationship between habitat and burrow type; and 4) the role of scale in management and conservation issues of burrowing seabirds.

6.1.1 The Hierarchical spatial distribution of seabirds' breeding habitat

The vast majority of vertebrate species live in heterogeneous environments produced either by physio-chemical factors, landscape factors and /or the availability of food, all of which may vary over space and time. However, population densities do not change in response to average conditions across a large habitat, as is assumed in classical non-spatial models, but rather in response to the local conditions experienced by each individual (Tilman & Kareiva 1997). In

many places, patchiness has increased over time due to degradation of habitat resulting in fragmentation. In fact, patchiness has become a characteristic of most species at most spatial scales (Kotliar & Wiens 1990).

Levins (1969) model of metapopulations was based on patches of suitable habitat for a species distributed over a landscape. Over time, colonisation of empty patches by animals from occupied patches and extinction of local populations on occupied patches occurs (Levins 1970). Extinction occurs due to changes in the environment affecting reproduction and mortality. Another type of metapopulation concept consists of local populations connected by dispersal, but without local populations becoming extirpated. This usually involves source-sink dynamics, whereby one patch is of sufficient quality (source) to sustain a population and the other is in a sub-optimal habitat (sink) which is topped up by migrants from the source habitat (Hanski 1994, 1998).

Metapopulation theory has also been applied to birds that are highly philopatric to their breeding colony or habitat patch, but understanding how independent subpopulations can be may require information about their spatial distribution throughout the annual cycle and local behavioural mechanisms that may lead to their demographic independence (Esler 2000). A metapopulation of little penguins has been identified for South-East Australia, but no strong phylogeographic structure was evident among 27 colonies from the Australian range of the species (Peucker *et al.* 2009). However, strong phylogeographic structure was found among 24 little penguin colonies in New Zealand supporting the existence of five sub-species, reflecting historic events, as a result, Peuker *et al.* (2009) concluded that little penguins at one time had very good dispersal potential and that population genetic connectivity existed among the colonies.

Can a hierarchy of metapopulations exist? Or does the proximity of colonies allow a certain amount of interaction amongst individuals across the populations, which then allows the existence of the network of populations? It could be argued that while little penguin populations around South East Australia form a single metapopulation at the geographical scale, the distribution of little penguins represented along the North West Tasmanian coast may be a smaller metapopulation at the *topo* scale.

Dispersal contributes to population growth, gene flow and species persistence, which makes it important in understanding population biology overall (Lowe & Allendorf 2010). Dispersal, and consequently connectivity, can be measured in two ways: genetically and demographically. Genetic connectivity has been demonstrated at the macro scale for little penguins, but pedigree analysis that can determine kinship among penguins in the 17 colonies in the study region or even between the two patches of penguin habitat at Doctor's Rocks remains to be undertaken (Chapter 2). The requirement of one migrant per generation for a genetic connection to be maintained among populations has been used for a long time, but it has been suggested that perhaps a minimum of one and a maximum of 10 migrants per generation would

be more appropriate (Mills & Allendorf 1996). For the study region, pedigree analysis would also be required to determine the genetic proximities among sub-populations.

An overview of connectivity shows how the concept has changed and become much broader (Kool *et al.* 2013) compared to the original idea of the maintenance of a terrestrial corridor (Taylor *et al.* 1993). Connectivity can now be defined as transport, dispersal and connectivity of marine organisms (Pineda *et al.* 2007), and hydrological connectivity (Pringle 2003), as well as demographic or genetic links (Lowe & Allendorf 2010). For many seabirds, connectivity amongst colonies at the *meso* scale is provided via the ocean (e.g penguins) or air (e.g. shearwaters) as seabirds use land only for breeding, roosting and occasionally moulting, and generally do not tend to cross terrestrial habitat to access other colonies.

In North West Tasmania, there may be overlap in the foraging areas during the breeding and non-breeding seasons, given the proximity of colonies along less than 50 km of coastline. It has been estimated that the average foraging distance during the breeding season at Phillip Island is within 30 km from their burrows (Collins *et al.* 1999; Bool *et al.* 2007) and during the non-breeding season from 42 to 48 km (Hoskins *et al.* 2008; McCutcheon *et al.* 2011). Dispersal of little penguins, whilst limited, occurs at sea once they have left the colonies. Some little penguins have been found to range up to 500 km from their colonies, but this is unusual (Collins *et al.* 1999). Emigration away from colonies is very low for little penguins as most movement takes place within 20 km offshore (Dann *et al.* 1992b; Norman *et al.* 1992). So it is quite likely that in this North West Tasmania population, encounters at sea, or through a propensity to investigate a nearby colony, might result in dispersal to other colonies. This may be linked to cues. For instance, the vocalisation of penguins just before they come on to land may be heard by penguins from other colonies swimming close by, resulting in their investigation of this potential new habitat. Further, demographically connected populations promote metapopulation stability by balancing birth, death and migration rates at two different spatial scales (Lowe & Allendorf 2010). At the individual population level ("colony" in this study) stability can be provided by the immigration of individuals into a population, compensating for a low birth or survival rate *i.e*. a sink population (Pulliam 1988; Runge *et al.* 2006).

At the metapopulation level, increasing colonisation of previously unoccupied patches can increase demographic connectivity even if currently occupied patches become extinct (Hanski 1998). This could occur in this study region where other unoccupied sections of habitat may be colonised from nearby populations. Also, it is hypothesised that demographic connectivity may in fact be increased in some of the 17 colonies that are in close proximity to each other, such as colonies 3 - 6, 7 - 10 and 11 - 15 (Table 2-4 in Chapter 2).

Sadly, the historical distribution of the colonies along the coastline is largely unknown. The current configuration could be either relicts of what were once larger colonies or they may have always been discrete entities. A study on highly philopatric black-headed gulls *(Chroicocephalus ridibundus*), a common breeding seabird in Europe, found that colonies were

significantly more frequent and larger in less- than more-fragmented landscapes (Kajzer *et al.* 2012). From the analysis of the 17 colonies along the coast at the *meso* scale in this study, it would seem that the presence of more frequent colonies may be the result of fragmentation due to anthropogenic factors. Fragmentation defined as splitting of continuous habitat into smaller patches, is different from habitat loss; however, the two are usually linked (Fahrig 2003) as the increase in urban development along the North West Tasmanian coast has led to not only the fragmentation of the habitat, but also the loss of potential habitat.

Development of the urban fringe gradually adds pressure onto native wildlife because of more roads, urban structures, ornamental vegetation, domestic animals and recreational use (Fleishman & Nally 2007). Four effects of fragmentation can be identified at a species level: loss of total amount of habitat, and increase in number, decrease in size, and increase in isolation of habitat patches (Fahrig 2003). In North West Tasmania, some little penguin colonies have disappeared and the number of little penguins within some colonies have decreased over the last decade in particular due to dog attacks; one beach, declared as a dog declared exercise area has a little penguin colony that has been decimated over the years due to dog attacks (P.Marker pers. obs.).

The extent of fragmentation on little penguins would need to be examined on a larger landscape scale than that used in this study (e.g. the entire North coast of Tasmania) to investigate further the potential effects of fragmentation on the persistence of little penguins. An index that characterises the size and shape of the colony, density of little penguin burrows and includes breeding success over time would need to be developed. The perimeter to area ratio (Table 2-5 Chapter 2) provides a coarse indication of the shape of the colony. The smaller the ratio, the larger the area for nest-sites within a colony and the less likelihood of exposure to predators.

6.1.2 The definition of a colony

The little penguins of North West Tasmania may represent a distinctive spatial arrangement, with 17 colonies along a 50 km stretch of coast in a mostly peri-urban distribution. A few other colonies exist in Australia in urban settings, such as St Kilda Breakwater in Melbourne, Manly Harbour in Sydney, and possibly Granite Island, although this last colony has decreased in size recently (Bool *et al.* 2007). However, a pattern dominated by closely spaced colonies such as in North West Tasmania appears to be rare. Wiebkin (2011) reported the occurrence of 19 colonies of little penguin on Kangaroo Island, South Australia during a survey in 1996, but these colonies were principally located in a coastal landscape then dominated by rural activities but these colonies are now greatly reduced.(Wiebkin 2011)

The initiation of the formation of a new little penguin colony in the natural environment has not been recorded. However, St Kilda, Victoria provides an example of a new colony formed on an artificial breakwater that was built in 1956 (Dann *et al.* 1996). Penguins from Phillip Island, 100 km away, which generally forage in Port Phillip Bay during spring and winter (Collins *et al.*

1999), formed this new colony some time before 1974 (Giling *et al.* 2008) in rocky boulders that provide good habitat for nesting penguins. This colony has increased over the years, to 1000 individuals in 2008, due to its close proximity to prey (<20 km) and an absence of predators, due to preventative measures (Preston *et al.* 2008). The St Kilda population is very closely linked to the Phillip Island colony, both genetically as well as demographically, and Phillip Island can be considered as the source colony (Overeem *et al.* 2008). Whether this is typical of colony formation is unknown, but the spatial scale of the linkage supports the probability that some of the colonies along the North West Coast could also be closely linked. Regular surveys for new colonies are suggested.

So what is a penguin colony? For adélie penguins *Pygoscelis adeliae*, a colony has been described as an assemblage of nesting penguins, or more specifically all the penguins breeding within a 4 km radius which are strongly related demographically; groups within the colony are called sub-colonies, *i.e.* a geographical definition (Ainley 2002; Dugger *et al.* 2010). Elsewhere, "colony" has been used to describe populations whose nest-site areas are contiguous with one another (Woehler *et al.* 1991; Woehler *et al.* 1994). Ainley's definition is independent of scale, and so accommodates the issues raised in Chapter 2. How distant do aggregations of penguin nests need to be before they are considered separate colonies or how close before they are considered sub-colonies of a larger population?

Adélie breeding penguins were found to disperse at a rate of 1% from their colonies in good years and at a much higher rate during poor years, even if environmental conditions inhibited migration, presumably to seek better breeding areas. Lowest rates of movements occurred among colonies at the greatest distance apart (Dugger *et al.* 2010). Similarly, studies with black-headed gulls (Peron *et al.* 2010) and European shags (*Phalacrocorax aristotelis*) showed that the greatest exchange occurred among colonies closest together (Brandl & Gorke 1988). Unsurprisingly, the main factor that determines whether a local population will be influenced by exact spatial relationships among patches is its dispersal distance, as found in a modelling study (Fahrig & Paloheimo 1988). If the average dispersal distance for a species is low relative to the average distance among patches, then the spatial pattern of habitat patches can have an important role of local population size. In the present study, 76% of the colonies were closer than 2 km to each other (Table 2-4, Chapter 2), which suggests that there might well be dispersal among the colonies and close genetic links at the pedigree level among penguins that needs investigation. The scale of independence of these colonies remains currently unresolved due to the lack of information on the genetic exchange and the movement among colonies in this region.

6.1.3 The relationship between habitat and nesting quality

Habitat quality and nest-sites have only been generally described in the past for little penguins in terms of the type of burrows (Klomp *et al.* 1991; Brothers *et al.* 2001; Stevenson & Woehler 2007). Terrain variables alone have not been used before to develop a model of habitat suitability for penguin. High resolution LiDAR DEMs are becoming more readily available. The high spatial resolution of the GIS data enabled a model that showed that burrow location was related to a positive, northerly facing slope with high solar radiation and a low wetness index value. This equates to a burrow that is warm, dry and able to be built into the ground. This model was able to predict 62% of the presence of burrows and 42% of the absence of burrows. This suggests that there was more available habitat which met the requirements of the model, but which was not used. Alternatively, this could also suggest that food availability was the limiting factor and not burrow habitat in the colonies. Other explanatory variables, such as vegetation type or cover that may affect microclimate of burrows could also be incorporated into the model which might increase its power in predicting the absence of burrows.

In the 11 colonies that were not included in the model, habitat quality remains unknown. Habitat quality in some of these colonies may be poor, and some may be sinks for others which are sources. Further, some of the closely adjacent small colonies (Chapter 2) may also be fragments of a larger colony split up by habitat degradation. Capture-mark-recapture of birds to monitor the frequency of movement among these colonies would provide insights into how the space is used and how much dispersal occurs. Long-term monitoring might also reveal the presence of ecological traps, which arise when organisms choose a poor quality habitat over better ones and for example, undergo negative population growth in areas that have undergone anthropogenic change (Schlaepfer *et al.* 2002; Battin 2004; Robertson *et al.* 2013).

In a peri-urban environment such as the study region, little penguins may be restricted (*e.g.* due to the presence of a fence) to modified landscapes that are in fact ecological traps. In an ecological trap, productivity is expected to be depressed relative to other areas, but this was not indicated by the chick productivity of two modified, peri-urban colonies at Doctor's Rocks and Parsonage Point (Chapter 5). A more comprehensive longitudinal study of breeding success that includes additional colonies along the coast is needed to establish if any of the colonies are ecological traps and which colonies may be sources or sinks.

The close proximity of the colonies along the North West Coast also suggests that overlap in foraging areas may occur, and consequently the size of these colonies may be limited by food resources. This could be consistent with the model developed for little penguins which integrates the effects of intra-specific competition for food and nesting sites in smaller sites (Dann & Norman 2006). Most little penguin colonies in Australia are small; 75% of colonies have <500 pairs (Dann *et al.* 1996; Dann & Norman 2006), but they are interspersed with a few very large

colonies. Whilst this might be related to central place foraging limitations, it could also be an indication of nesting quality and suitable habitat availability. Assessment of breeding success among colonies of different sizes along the coast would provide insights into the influence of these variables.

Overall, the patch-like network of colonies suggests that in evolutionary terms an ideal free distribution model might fit the observed pattern (Fretwell & Lucas 1970; Krivan *et al.* 2008). This model looks at frequency dependent animal distribution. It assumes that individuals are "ideal" and consistently settle in the habitat where their fitness is maximised. Thus they are "free" in their choice of habitat site so that all individuals within a habitat have an equal expected fitness (Brown & Rannala 1995). Over time a more equitable population in the colonies should result. One of the driving forces for this is the availability of food, and if the ideal free distribution model holds, then the dispersion pattern of predators (penguin colonies in this case) tends towards regular, so that equal access to food is likely for each of the birds in the colonies (Sutherland 1983). However, the phenotypic variability of individuals, which results in different hunting and consequently consumption abilities, plus the variation in local environmental conditions, may influence the ability of individual penguins to raise chicks. This in turn could influence the success of the colonies to persist in their location. In addition, the foraging zone is likely to be a competitive zone among the foragers from different colonies so that as the density of foragers increases there could be increasing use of lower quality patches (Tregenza *et al.* 1996) which would have an influence on the "fitness" of some of the colonies.

A number of characteristics were identified as being typical of penguin nesting habitat: a large enough area for nest-sites within a colony to minimise exposure to predators, north facing nest-sites, dry soil conditions, access to the coast, moderate slopes, suitable micro-climate (not too warm or too humid), and nest cover of some form. When these factors are optimised they should result in successful chick production, and as a result, other things being equal (such as adult longevity and low mortality rates), increasing population growth. The listed characteristics can be typical of many types of landscape forms from natural to highly modified types, as seen in a number of the colonies in this study, and may apply to other burrowing seabirds, although species specific-factors would lead to variation.

Every seabird selects a nest-site within a location based on a variety of ultimate or proximate factors, each of which has spatial and temporal components. Little penguins were found in nest-sites underground in burrows dug into the sand, in rock hollows scattered along the shoreline, above ground under vegetation such as shrubs, vines and grass, and in a range of artificial burrows such as concrete igloos, black plastic pipe and various other materials. Chick production occurred successfully in sand, vine, grass and artificial burrows indicating that these nests types at least supplied the minimum requirements for breeding (Chapter 5). However, chick productivity was highest in artificial burrows, the microclimate of which was significantly different from the other types (Table 6-1). The mean temperature of artificial burrows (19.22 ±

1.63^{0}C) was 1-2^{0}C higher than in natural burrows and was significantly different from all other burrow types (Table 6-1). Similarly the mean relative humidity of artificial burrows (77.2 ± 7.4%) was 8% lower than in other burrow types and relative humidity was significantly different among burrow types (Table 6-1).

This raises some interesting questions as to whether artificial burrows should be used at all, and whether leaving penguins to source nest-sites from available materials is more appropriate. However, as the landscape has been modified due to anthropogenic influences it could be argued that the availability of natural nesting sites has been compromised already, and that artificial nests are offering penguins suitable alternatives. The importance of artificial nesting sites to the populations would be if the colony in which they were used grew significantly faster than colonies where they were absent or fewer in number. The use of artificial burrows as a conservation tool will be discussed further in the last section.

Burrow productivity does not seem to be solely determined by the differences in temperatures and relative humidity among the different burrow types as all are used successfully within this limited, two colony study, suggesting that little penguins have a wide tolerance to temperature and humidity. However, with the increasing temperatures predicted as a result of climate change, it is relevant that the number of hours > 27^{o}C was significantly different for each burrow type. Artificial burrows maintained this temperature proportionally longer than the other burrow types over the study period. Temperatures > 27^{o}C are above the Upper Critical Temperature (UCT) for little penguins and lead to an increase metabolic activity (Stahel & Nicol 1982), yet artificial burrows led to the highest chick productivity in little penguins, at least in this study. Whether this can be sustained if the UCT is exceeded more often remains to be seen.

Table 6-1 *Summary of results for each burrow type in this study from Chapter 2, 4 and 5. Artificial burrows are higher in mean temperature and lower in relative humidity, but higher in the mean number of chicks produced per year. The nearest neighbour is not a useful index for artificial burrows as they are placed by humans.*

Burrow type	**Mean nearest neighbour distance ± SE (n)**	**Mean temperature ± SE ^{0}C (n)**	**Mean relative humidity ± SE % (n)**	**Percentage of burrows temperatures above UCT (27^{0}C)**	**Productivity of burrows Mean number of chicks /burrow year ± SE (n)**
Artificial	2.86 ± 0.107 (347)	19.2 ± 1.64 (14)	77.2 ± 7.41 (5)	11.15	0.65 ± 0.04 (n)
Grass	3.31 ± 0.222 (153)	17.2 ± 1.06 (13)	85.2± 7.38 (3)	1.67	0.27 ± 0.08 (n)
Sand	3.00 ± 0.121 (445)	18.6 ± 1.26 (12)	93.4 ± 5.36 (4)	4.1	0.39 ± 0.05 (n)
Vine	1.87 ± 0.078 (293)	17.2 ± 1.22 (17)	83.5 ± 7.96 (4)	3.5	0.40± 0.08 (n)

Interestingly, vine burrows were the most closely spaced (average inter-nest distance 1.87m) (Table 6-1). Mean temperatures of these burrows was 17.2 ± 1.22^{0}C , which was the lowest mean temperature of the burrow types, and mean relative humidity of 83.51 ± 7.96%, the second lowest relative humidity of burrow types (Table 6-1). However, while the burrow density suggests that vines are attractive to the adults, their burrow productivity (0.40 chicks per year), whilst second to the artificial burrows, was not significantly higher than other types of burrows. The spacing of burrows may reflect the structure of the vegetation and the amount of cover rather than a preference by penguins for any particular type of vegetation. The microclimate of burrow types incorporated into this study provides another measure that may provide insights into habitat quality. Microclimate has been shown to be important; experimental work using heat pads suggests that, from a thermal perspective, the avoidance of heat stress is an important and underappreciated issue in the nest-site selection of endotherms (Kearney *et al.* 2011).

The degree of clustering of burrows varied among different vegetation types but it may not be an indication of habitat quality (Van Horne 1983; Johnson 2007; McVinish & Pollett 2013). Habitat quality is a key contributor to an individual's fitness if the species is to occupy habitats over a long time (Block & Brennan 1993). To unravel the role of habitat quality requires habitat-specific measures of demography such as density, reproduction and survival in each habitat considered (Johnson 2007). Habitat quality is typically evaluated as "good" or "poor", depending on the breeding success of the species. However, quality could also depend on whether

assessment is made at the individual or population level. Long-term assessment would also provide some insights as to whether different burrow types are more advantageous in different seasons when climatic factors may vary, or if the breeding season commences early.

Johnson (2007) modelled two hypothetical habitats, where Habitat A had few high-quality resources and Habitat B had abundant but lower-quality resources (resources could be nest-sites or prey). At the population level, Habitat A would offer the higher intrinsic rate of population growth as the selection of fit individuals would be advantaged, whereas Habitat B would have the higher carrying capacity so that it would always support a higher population. For individuals, Habitat A would offer higher quality resources which would benefit the species and increase their chances of survival and reproduction as a function of natural selection. However, at the population level, Habitat B may be better as it supports a larger persistent population (Johnson 2007).

Another closely associated issue is a residual reproductive value which represents an organism's future reproduction potential through its investment in growth and survivorship. So investing in good resource characteristics (e.g. selecting suitable burrows) can enhance the survival and future reproductive potential of the parents. This could be an important aspect in relation to the type of burrows used for conservation and management. For instance, artificial burrows have been shown to have a positive relationship with chick production in this study and over a longitudinal study may be shown to have a high residual reproductive value.

Multiple indicators such as body condition and other biological indicators are also important aspects of habitat quality, since conditions that favour density, survival and reproduction are not necessarily the same (Johnson 2007). This study on little penguins illustrates how nest-site characteristics such as the construction material, microclimate, and the number of chicks produced from each type of burrow can indicate burrow quality. However, year to year temporal variations, duration of site fidelity and lifetime reproductive success need to be considered in a long term study as it will have implications for the selective value of the habitat and burrow type.

6.1.4 The role of scale in management and conservation issues of burrowing seabirds.

Little penguins are not a formally listed threatened species in Tasmania, but some populations of penguins are threatened by their location in urban and peri-urban areas where anthropogenic pressures have resulted in a loss of local populations (Chapter 1). In this region all 17 colonies are located in urban and peri-urban areas. These colonies, apart from providing tourist opportunities, are also part of the South East Australia metapopulation (Peucker *et al.* 2009).

It is often considered that species that are not threatened require little or no management, especially in a time of shrinking resources and capacity and when priorities need to be considered. In fact, these species can often be well managed with little effort compared to more threatened species. However, where necessary it is always cheaper to undertake proactive

measures rather than reactive *post-hoc* repair jobs, even for species that are not currently listed as threatened.

Two major drivers for the decreasing populations of seabirds worldwide are habitat loss (Croxall *et al.* 2012) and climate change (Chambers *et al.* 2011). The challenge for conservation is to maintain functioning ecosystems. This depends on a number of factors such as the habitat area, quality and aggregation (Hodgson *et al.* 2011), with variations in habitat area and quality having greater effect than variations in the spatial arrangement of habitat or corridors.

Much conservation work takes place at the local patch scale, which may mask the decrease of the species in a regional context if the focus is on a single area, for example, in sink habitats that are not self-sustaining (Brawn & Robinson 1996). Edge effects and fragmentation may also lead to habitat loss, so being able to determine the degree to which these can be tolerated by a species may help in its overall conservation and management. This was modelled in a study using Henslow's sparrow (*Ammodramus henslowii*) which identified thresholds in persistence which were dependent on edge sensitivity; however the study did warn against using prescriptive rules in conservation (With & King 2001).

In another example, where the common tern (*Sterna hirundo*) inhabits the Rhine-Meuse-Scheldt estuary, port and harbour areas were considered to be separate populations of a metapopulation. In this case, modelling of newly created breeding habitat was used to design replacements for lost habitats and so prevent extirpation (Schippers *et al.* 2009). This study concluded that new locations should be selected not only based on suitability of habitat, but also proximity to suitable food areas.

Spatial and temporal scales used in conservation need to be taken into account. For instance the same ecological process may exhibit different patterns if observed and analysed at different scales. Species' behaviour may also operate at different scales, e.g. the foraging behaviour of seabirds can take place in a range from a few metres distance from the colony to kilometres distance, compared to the breeding site, which is usually a static point for a certain amount of time. This makes predictions across scales difficult in the conservation and management of wide-ranging species like many seabirds. So managing and matching colonies to vegetation types may need to consider the appropriate microclimatic conditions, and also take into account the location of foraging areas and whether protection of foraging areas is required to support a given size of the population.

A shift in conservation efforts in the anthropogenic modified landscape, from the local (patch areas such as colonies) to the landscape (ecological networks such as a regional approach) scale should be considered (Baguette & Mennechez 2004). However, landscapes, or habitat patches within the landscape, can change over time through succession, and this may have a role in changing the distribution of colonies. It has been suggested that if the number of reserves is sufficiently large then the complexity of selection of different candidate sites could be ignored and that individual selections could be made independently (Drechsler *et al.* 2009). While this

model may be appropriate for succession in natural communities, the little penguin colonies in this study are in highly disturbed and variable areas which have nonetheless persisted through time. Selection based on individual characteristics of the sites might be useful but perhaps omits the metapopulation dynamics that may be important too.

There are two aspects to habitat patches that need consideration. Firstly, it could be that patches of habitat with different characteristics have always been present in the landscape, particularly along the North West Coast, and little penguins have adapted to the availability of suitable patches. Secondly, the patchy nature of habitats has developed over time through anthropogenic pressures and has resulted in fragmentation of colonies posing some interesting problems in terms of conservation. It has been found that the importance of a patch depends not only on the properties of the landscape, but also on the properties of the species (Dunning *et al.* 1992; Ovaskainen & Hanski 2003). More importantly, variation in the importance of fragments is greatest in the case of rare species that occur close to the extinction threshold, as they are likely to be restricted to the most favourable fragments of the landscape (Ovaskainen & Hanski 2003), whereas with a more abundant species such as little penguins, a much wider range of patches within fragments can be used.

Seabird conservation has used many strategies at the individual- and colony-scale, such as the use of artificial nest boxes to compensate for habitat loss *e.g.* little penguins (Ropert-Coudert *et al.* 2004), yellow-eyed penguins (Lalas *et al.* 1999), and African penguins (Kemper *et al.* 2007; Sherley *et al.* 2012). Re-location of species to new habitats has also been a successful counter measure to re-balance the loss of the species, *e.g.* Gould's petrel *(Pterodroma leucoptera leucoptera*) with the use of artificial burrows (Priddel *et al.* 2006), and common diving petrels (*Pelecanoides urinatrix*) on Mana Island, New Zealand with the use of acoustics to attract the petrels (Miskelly & Taylor 2004).

The translocations of eight other species of petrels has also been successful within the New Zealand region (Miskelly *et al.* 2009). All of these strategies operate on individual colonies and nest-sites, but rarely consider colonies in a region to identify any source, sink or ecological traps of the species under investigation. It could be argued that when dealing with a single species whose population is decreasing such measures may be necessary. However, the results of this study suggest that in geographical areas where a species may be widely distributed, selecting all colonies for management support may not be logistically possible or the most appropriate use of time and available resources.

The following questions can be raised within the context of conservation efforts for seabird colonies.

- Should larger colonies be supported at the expense of smaller colonies?
- Are all colonies genetically and demographically linked and hence have some synergistic role as part of the whole metapopulation?
- Which colonies have the greatest chance of persistence?

These questions pose interesting potential dilemmas and have led to the current practice of conservation triage that is gaining more traction for threatened species (Bottrill *et al.* 2008; McDonald-Madden *et al.* 2008). Priority decisions are made by scoring the likelihood of success (usually the persistence of a species) against a set of criteria, including costs, which are usually set by a manager responsible for allocation of resources. Participation of stakeholders can also result in difficult decisions being made about strategy, including one that is accepted as not being the best in purely conservation terms.

An evidence-based process may result in better decisions no matter whether the species, or just some populations, is threatened. For instance, measuring productivity, density and other variables among the colonies over time may provide insights into which colonies are more successful. A flexible approach to resource allocation among colonies may then lead to better results in, say, their persistence. However, a difficulty arises if the colonies are part of a synergistic network that contributes to species persistence in a region. Selection of one or two colonies via the triage method may then not be the best solution.

If the appropriate information is used along with the framework illustrated in Figure 6-1, then some habitats could be changed from one type to another by the flexible use of resources and mitigation strategies. As a conservation tool this could result in reduction of the negative effects of unsuitable habitats or ecological traps. Gilroy and Sutherland (2007) and references therein applied this model to several examples of avian fauna. They found that experimental manipulation such as removal of settlement cues or the introduction of cues to undervalued resources cannot be effective measures in increasing species persistence.

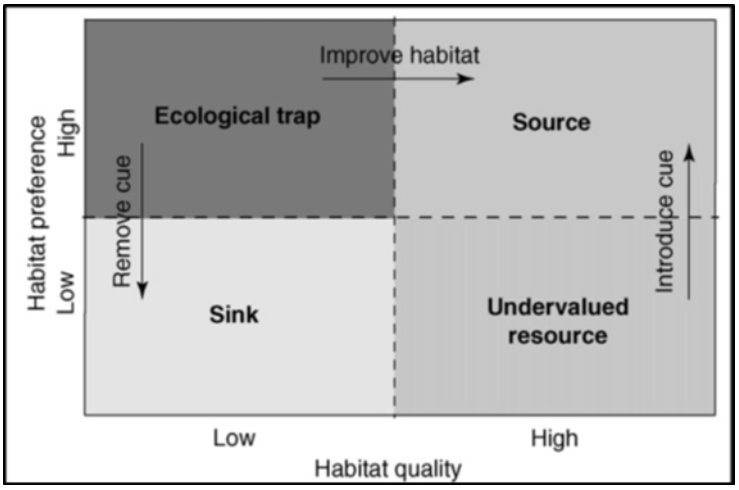


Figure 6-1 *A framework actions that could decrease the negative effects of ecological traps. Improving habitat discourages settlement in the ecological trap areas and focuses on alternate habitats which may offset the poor effects of the ecological trap (Gilroy & Sutherland 2007).*

Based on the findings of this study, some recommendations can be made to assist the conservation and management of little penguins at the micro scale level in modified and degraded landscapes. Firstly, habitat suitability mapping provides an understanding of the environmental variables that may be appropriate for identifying areas that are suitable for a species. Secondly, artificial burrows with sufficient holes to ensure good ventilation and prevent overheating in warmer weather, promote high chick productivity and make suitable alternatives to natural burrows. They have been used in many of the colonies along the North West Coast as a supplement for lost habitat because of coastal development, erosion and predation. However, the placement of artificial burrows in the colonies in relation to terrain characteristics certainly needs more careful consideration.

Thirdly, rehabilitation of degraded areas with native vegetation needs to be carefully considered in the context of the type of cover and the microclimate that results. For example, one of the six colonies (Sulphur Creek, Figure 2-8) has a very dense covering of vines in one section. These vines are all introduced species / exotic weeds and their removal and rehabilitation of the site to native species might be considered a good outcome from one perspective. But, from the penguin's point of view, this vegetation currently provides adequate cover, a suitable microclimate, and a large enough area for chick production. Thus simply considering vegetation characteristics to infer habitat quality based on density of penguins can be misleading with regard to population growth.

The use of conceptual models provides a novel way of looking at spatial scale at different levels of little penguin aggregation. As in the Introduction, Figure 6-2 outlines the key factors that operate at the different habitat scales and what the successful indicators of persistence of a species might be at each spatial level for the little penguin. The hierarchical spatial scale of habitat is represented by symbols starting at the global or geographic scale and then progressing to the smallest *nano* scale of individual birds at the nest-sites. The key abiotic and biotic factors that might operate and influence the distribution of the level of organisation are suggested on the left hand side, but that is not to say their sphere of influence is restricted to the one spatial scale. For instance, whilst oceanic factors and sea level temperatures may influence all levels, their major scale of influence is most likely global. The indicators of persistence of little penguins are suggested on the right hand side and are targets that could be aspired to in an ideal or theoretical world.

Figure 6-3 takes these relationships one step further and indicates, at each of the habitat spatial scales, what metrics could be used to assess the abiotic and biotic factors operating at each level. These can assist with the analysis and understanding of the spatial ecology of little penguins e.g. their tracking from different colonies at the *meso* scale identifies not only foraging areas, but also the proximity of the foraging area of the colony. Management options that might be adopted to help with the persistence of the habitat level at each scale as represented in Figure 6.2 are indicated on the right hand side of Figure 6-3.

Key factors operating at different habitat scales

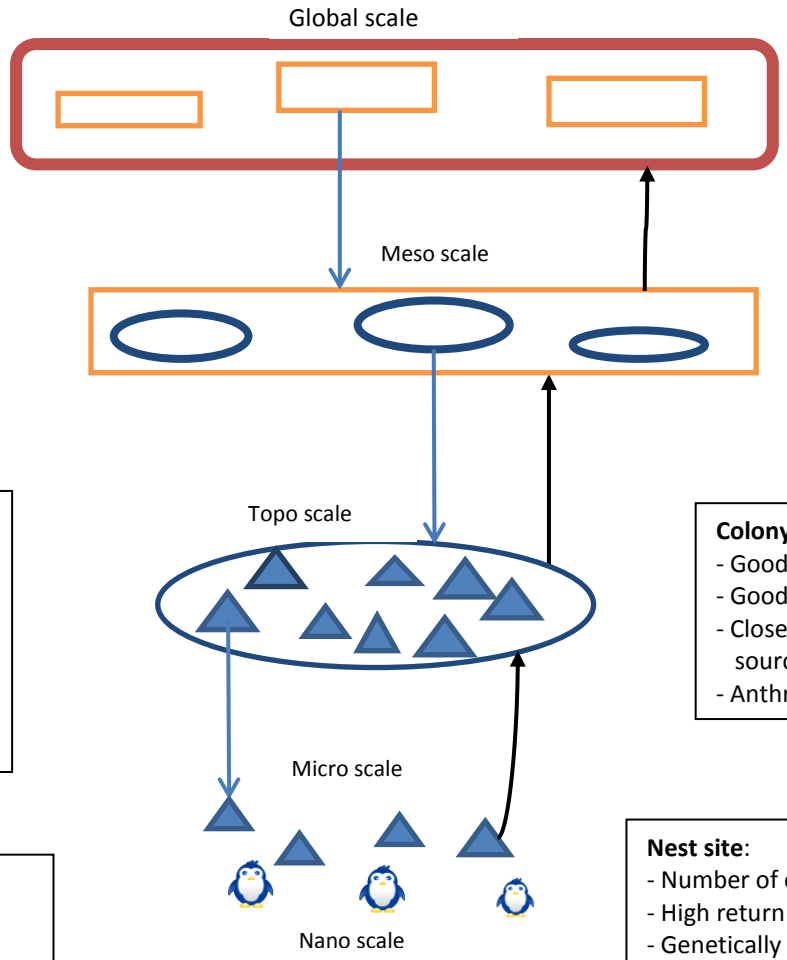
- Oceanographic factors
- Temporal changes in sea surface temperature / productivity
- Geographic landscape factors

- Spatial distribution of colonies
- Proximity to foraging zones
- Regional climate factors
- Human activities – fishing pressures

- Topographic variables
- Type of vegetation
- Predators
- Social interaction
- Use of colony by other species / interspecific competition
- Anthropogenic pressures
- Erosion / loss of habitat

- Types of burrows
- Microclimate - temperature, humidity
- Density dependent factors e.g. ecto parasites
- Fitness of individuals – natural selection

Habitat spatial scale



Successful indicators of persistence

Geographical zone:
-Persistence in regions over time of metapopulations

Regional geographical zone:
-Persistence of colonies over time

Colony:
- Good microclimate of burrow types,
- Good habitat characteristics
- Close proximity to food sources and sufficient food sources
- Anthropogenic pressures minimised

Nest site:
- Number of chicks fledging each year is high.
- High return of adults to colony for future breeding.
- Genetically fit individuals

Figure 6-2 *Model of key factors operating at different habitat scales and what successful indicators may look like. The habitat spatial scale is represented by the shapes; the top brown box represents the* global *distribution of a species (little penguin distribution in Australia and New Zealand); the next or* meso *level is represented by the regional distribution (the North West Coast Tasmania study area of little penguins); the blue oval or the* topo *scale is represented by the colony (an example could be one of the six study colonies); the blue triangles represents the* micro *scale at the nest site (burrow) and at the* nano *scale the individual bird (penguin).The left hand side outlines the key factors that influence the habitat spatial scale, commencing with factors that have a large scale influence such as sea temperature at the geographic distribution of a species, to small local factors such as microclimate of burrows that influence survival of chicks at the* nano *scale. The right hand side provides the ideal indicators of persistence of a species at the different spatial levels commencing at the nest site and working back up to the geographic level.*

Key metrics that can be measured at different habitat scales

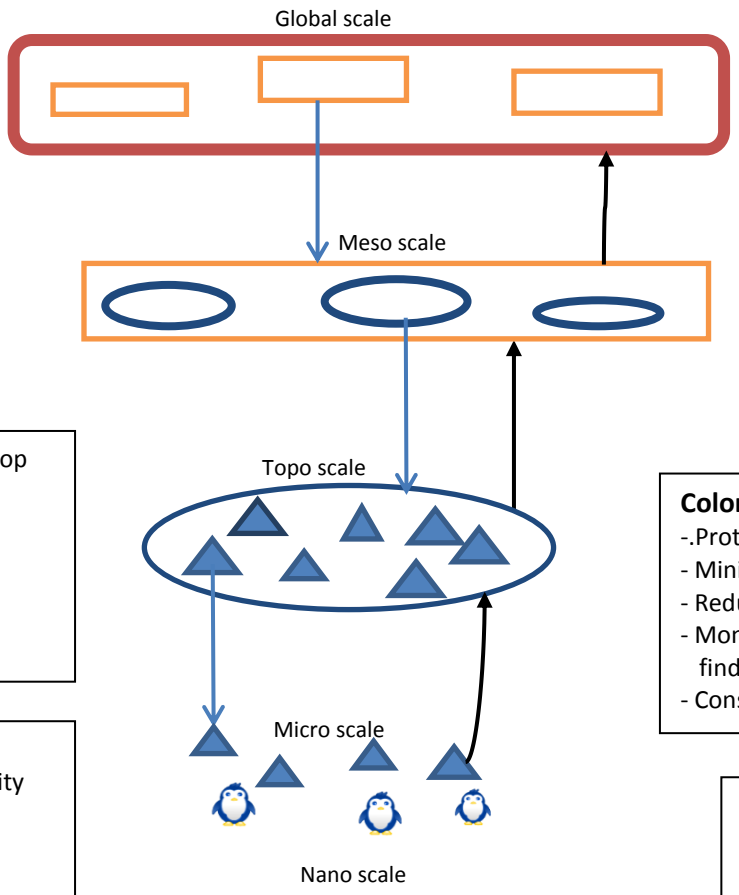
- Oceanographic currents
- Sea surface temperatures
- Chlorophyll distributions
- Metapopulation approach to identifying food zones

- Proximity to foraging zones by tracking penguins
- Regional climate variables from meteorological records

- Measure terrain variables from DEM and develop habitat model
- Identify types of vegetation (including invasive weeds)
-Map extent of colony boundaries
-Map vegetation to assess possible density of burrows

- Measure density among types of burrows
- Measure micro climate – temperature / humidity among burrows
- Measure density dependent factors e.g. ecto-parasites
- Measure breeding / reproductive parameters

Habitat spatial scale



Suggested management strategies

Geographical zone:
- Identify other ecosystem components
- Identify Marine Protected zones depending on species composition
- Provide management plans to protect foraging areas from anthropogenic activities

Regional geographical zone:
- Establish sustainable fishing around regions
- Evaluate effect of gill netting colonies
- Develop management protocols re dogs and cats

Colony:
-.Protection from invasive predators
- Minimise number of tracks for humans to access
- Reduce presence of rabbits in colonies
- Monitor and remove the types of weeds that penguins find difficult to penetrate
- Consider what vegetation is appropriate in each colony

Nest site:
-Assess suitability of burrows, supplement with artificial burrows where required
- Provide fire resistant artificial burrows
- Use habitat model to site burrows

Figure 6-3 *Model of key metrics that can be used to measure success at different habitat scales and what successful management may look like at each habitat scale. Metrics that can be measured at each of the habitat scales are indicated on the left hand side commencing at the large scale global distribution level and progressing down to the fine scale at the nest site level. The right hand side provides some management measures that could be considered appropriate from the nest site up to the geographic zone using evidence for best management practices.*

6.1.5 Future directions for little penguin research

This study raises many questions with respect to the breeding distribution of little penguins and further avenues of research. These will require long-term monitoring of contrasting colonies over a number of breeding seasons to identify which are sources, sinks or ecological traps. The following research directions are suggested:

1) Identifying foraging zones and their proximity to the colonies. Do foraging zones overlap; do colonies share foraging zones? If they are sharing the same zone, does this indicate that the colonies are more closely linked than if they were not overlapping?
2) Genetic pedigree analysis to measure which colonies are more closely related to each other, to give an indication of how many colonies there may be in the region;
3) Measuring coastal shorelines and monitoring changes over time to identify rate of loss of habitats and also surveying the coast for new colonies;
4) Modelling impacts of climate change; modelling the effect of increased temperatures on microclimate of burrows;
5) Developing better predictive habitat suitability models to be able to maximise available habitat options for little penguins.

The persistence of these colonies on the North West coast is due in part to many volunteers working in partnerships with the local land managers (Councils, Parks and Wildlife Service and local NRM). With further careful planning, investment and knowledge, this should be allowed to continue.

7 References

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8 Appendices

8.1 Appendix 1 Global Positioning System

The Global Positioning System (GPS) has been under development since 1973 and has been fully functional since the mid-1980s. Global Navigation Satellite Systems (GNSS) is a collective term for navigation systems that provide three dimensional positioning solutions by passive ranging using radio signals transmitted by orbiting satellites (Awange 2012). This now encompasses many systems such as Global Positioning System (GPS), Russian GLONASS, European GALILEO and the Chinese Beidou systems. GNSS provides a basic radial positioning accuracy of 1.3 – 3.9 m in the horizontal and 1.6 – 6.3 m in the vertical axes, depending on various aspects such as service, receiver design, and unit and signal geometry (Groves 2013).

There are three elements to the use of a GPS: the space, control and the user element. The space segment consists of 24 satellites arranged in six orbital planes above the earth's surface. Each plane is inclined about 55^{o} to the equator and hosts four satellites, which is why at least four satellites are always visible simultaneously at any given time. The control segment contains a network of five globally distributed monitor stations located around the world which is responsible for maintaining GPS time by a set of atomic clocks and satellite clock corrections. Satellite orbits are expressed in the earth- centred, earth-fixed (ECEF) World Geodetic System 1984 (WGS84). The user segment consists of the entire range of hardware, software and operational procedures available to collect and process GPS data. It also contains the infrastructure such as civilian reference stations that assist in increasing the systems accuracy when using a differential GPS (DGPS) such as the continuously operating reference stations (CORS) (Janssen 2010).

In Tasmania, DGPS does provide greater accuracy and precision in recording the placement of single point observations in the landscape than a handheld GPS or mapping points onto an arbitrary grid, but a base station and receiver are required. The ProMark 3 single-frequency RTK Differential GPS (DGPS) system uses two GNSS antennae, one as a static point at a known location referred to as the base station, the other attached to a back pack on the recorder known as the rover. Single-frequency RTK mapping measures the position of the two antennae relative to each other in real time. DGPS minimises most GPS errors because it makes frequent corrections to field errors such as decorrelation with time (satellite clock errors, ephemeris [orbit] errors , ionospheric and tropospheric errors) and distance (satellite ephemeris, ionospheric and tropospheric errors) (Monteiro *et al.* 2005).

8.2 Appendix 2 Species list from the North West Coast colonies.

Species list of plants found and recorded at burrow locations.

Common name of vegetation	Species name	Category
Bracken	*Pteridium esculentum*	Fern
Marram Grass	*Ammophila arenaria*	Grass
Onion Weed	*Asphodelus fistulosus*	Grass
Sedge	*Carex* sp.	Grass
Tasman Flax Lily	*Dianella tasmanica*	Grass
Knobby Club Sedge	*Ficinea nodosa*	Grass
Rush	*Juncus* sp.	Grass
Sagg	*Lomandra longifolia*	Grass
Thistle	*Onopordum acanthium*	Grass
Tussock grass	*Poa* sp.	Grass
Sea Wheatgrass	*Thinopyrum junceiforme*	Grass
Watsonia	*Watsonia* sp.	Grass
Buzzy	*Acaena* spp.	Herb
Wild Turnip	*Brassica barrelieri*	Herb
Sea Rocket	*Cakile maritima*	Herb
Milkweed	*Gomphocarpus fruticosus*	Herb
Fire Bush	*Senecio prenanthoides*	Herb
Coastal Wattle	*Acacia longifolia var. sophorae*	Shrub
African Daisy	*Arcotis stoechadofolia*	Shrub
Silver Banksia	*Banksia marginata*	Shrub
Prickly Box	*Bursaria spinosa*	Shrub
Native Currant	*Coprosma quadrifida*	Shrub
Mirror Bush	*Coprosma repens*	Shrub
Correa	*Correa alba*	Shrub
Cotoneaster	*Cotoneaster* sp.	Shrub
Broom	*Cytisus scoparius*	Shrub
Sea Spurge	*Euphorbia paralias*	Shrub
Cushion Plant	*Leucophyta brownii*	Shrub
Currant Bush	*Leucopogon parviflorus*	Shrub
African Boxthorn	*Lycium ferocissimum*	Shrub
Mallow	*Malva* sp.	Shrub
Coastal Boobyalla	*Myoporum insulare*	Shrub
Coastal salt bush	*Rhagodia candolleana*	Shrub
Sweet Briar	*Rosa rubiginosa*	Shrub
Blackberry	*Rubus fructicosus*	Shrub
Wild Raspberry	*Rubus parviflorus*	Shrub
Kangaroo Apple	*Solanum laciniatum*	Shrub
Gorse	*Ulex europaeus*	Shrub
Blackwood	*Acacia melanoxylon*	Tree
She Oak	*Allocasuarina* sp.	Tree
Gum tree sp.	*Eucalyptus* sp.	Tree
Tea Tree	*Leptospermum* sp.	Tree

Swamp Paperbark	*Melaleuca ericifolia*	Tree
Pine Tree	*Pinus radiata*	Tree
Rambling Dock	*Acetosa sagittata*	Vine
Pigface	*Carpobrotus* sp.	Vine
Cape Ivy	*Delirea odorata*	Vine
Honeysuckle	*Lonicera periclymenum*	Vine
Pampas Lily Of Valley	*Salpichroa origanifolia*	Vine
Bower Spinach	*Tetragonia implexicoma*	Vine
Periwinkle	*Vinca major*	Vine

8.3 Appendix 3 Results of trials

Trial 1

Candidate models	Np	AIC	ΔAIC	wAIC
B~ Slope +Aspect + Solar + WIndex	**5**	**4559.4**	**0.0000**	**0.39739**
B~ Slope+Solar+WIndex	3	4559.8	0.4778	0.31294
B~ Elevation + Aspect + Slope +Solar + WIndex	6	4561.4	1.9911	0.14685
B~ Elevation + Slope +Solar + Windex	5	4561.9	2.4764	0.11521
B~ (null)	1	4624.5	65.1211	2.87311×10^{-15}

Np: number of parameters, AIC: Akaike's Information Criterion, **Δ**AIC: difference in AIC from that of the best fitting model, *w*AIC: AIC weight

Trial 2

Candidate models	Np	AIC	ΔAIC	wAIC
B~ Slope +Aspect + Solar + WIndex	**5**	**4576.7**	**0.0000**	**0.48509**
B~ Elevation+Aspect+Slope+Solar+WIndex	6	4578.7	1.9997	0.17848
B~ Slope +Solar + WIndex	4	4579.3	2.6312	0.11306
B~ Slope +Aspect +Windex	4	4580.0	3.3649	0.01864
B~ (null)	1	4628.7	52.0227	2.4504×10^{-12}

Np: number of parameters, AIC: Akaike's Information Criterion, **Δ**AIC: difference in AIC from that of the best fitting model, *w*AIC: AIC weight

Trial 3

Candidate models	Np	AIC	ΔAIC	wAIC
B~ Slope +Aspect + Solar + WIndex	**5**	**4576.8**	**0.0000**	**0.35208**
B~ Slope +Aspect + WIndex	4	4577.7	0.9487	0.21908
B~ Elevation + Aspect + Slope +Solar + WIndex	6	4578.2	1.4443	0.17100
B~ Elevation + Aspect + Slope + Windex	5	4579.6	2.8155	0.08615
B~ (null)	1	4628.7	51.9240	1.8684×10^{-12}

Np: number of parameters, AIC: Akaike's Information Criterion, **Δ**AIC: difference in AIC from that of the best fitting model, *w*AIC: AIC weight

Trial 4

Candidate models	Np	AIC	ΔAIC	wAIC
B~ Slope +Aspect + Solar + WIndex	**5**	**4567.5**	**0.0000**	**0.6666**
B~ Elevation + Aspect + Slope +solar + WIndex	6	4569.5	1.9358	0.25324
B~ Slope + Aspect + WIndex	4	4572.9	5.4105	0.04456
B~ Elevation + Aspect + Slope + Windex	5	4574.8	7.3114	0.07227
B~ (null)	1	4628.7	61.1610	3.4909×10^{-14}

Np: number of parameters, AIC: Akaike's Information Criterion, **Δ**AIC: difference in AIC from that of the best fitting model, *w*AIC: AIC weight

Trial 5

Candidate models	Np	AIC	ΔAIC	wAIC
B~ Slope + Solar + WIndex	**4**	**4581.8**	**0.0000**	**0.21091**
B~ Slope +Aspect + Solar + WIndex	5	4582.2	0.3821	0.17423
B~ Slope + WIndex	3	4582.2	0.7331	0.14616
B~ Slope +Aspect + Windex	4	4582.5	3.7600	0.06590
B~ (null)	1	4628.7	46.8801	1.39377×10^{-11}

Np: number of parameters, AIC: Akaike's Information Criterion, **Δ**AIC: difference in AIC from that of the best fitting model, *w*AIC: AIC weight

Trial 6

Candidate models	Np	AIC	ΔAIC	wAIC
B~ Slope +Aspect + Solar + WIndex	**5**	**4577.9**	**0.0000**	**0.34079**
B~ Elevation + Aspect + Slope +Solar + WIndex	6	4578.8	0.9330	0.21374
B~ Slope +Aspect + WIndex	4	4579.6	1.7031	0.14543
B~ Slope +Solar + Windex	4	4580.2	2.3739	0.01039
B~ (null)	1	4630.1	52.1996	1.5758×10^{-12}

Np: number of parameters, AIC: Akaike's Information Criterion, **Δ**AIC: difference in AIC from that of the best fitting model, *w*AIC: AIC weight

Trial 7

Candidate models	Np	AIC	ΔAIC	wAIC
B~ Slope + Solar + WIndex	**4**	**4568.7**	**0.0000**	**0.37996**
B~ Slope +Aspect + Solar + WIndex	5	4569.3	0.6136	0.27956
B~ Elevation + Slope +Solar + WIndex	5	4570.7	1.9827	0.14099
B~ Elevation + Aspect + Slope +Solar + Windex	6	4571.3	2.5830	0.10443
B~ (null)	1	4625.9	57.2058	1.4377×10^{-13}

Np: number of parameters, AIC: Akaike's Information Criterion, **Δ**AIC: difference in AIC from that of the best fitting model, *w*AIC: AIC weight

Trial 8

Candidate models	Np	AIC	ΔAIC	wAIC
B~ Slope +Aspect + Solar + WIndex	**5**	**4549.464**	**0.0000**	**0.32979**
B~ Elevation + Aspect + Slope +Solar + WIndex	6	4550.3	0.8235	0.21848
B~ Slope +Solar + WIndex	4	4550.4	0.8886	0.21149
B~ Elevation + Slope +Solar + Windex	6	4551.0	1.5199	0.15423
B~ (null)	1	4627.3	58.073	1.54239×10^{-18}

Np: number of parameters, AIC: Akaike's Information Criterion, **Δ**AIC: difference in AIC from that of the best fitting model, *w*AIC: AIC weight

Trial 9

Candidate models	Np	AIC	ΔAIC	wAIC
B~ Slope + Solar + WIndex	**4**	**4581.9**	**0.0000**	**0.33694**
B~ Slope + WIndex	3	4583.3	1.3322	0.17309
B~ Slope+ Aspect + Solar + WIndex	5	4583.6	1.7050	0.14365
B~ Elevation + Slope +Solar + Windex	5	4583.9	1.9811	0.12513
B~ (null)	1	4628.7	46.7359	2.3932×10^{-11}

Np: number of parameters, AIC: Akaike's Information Criterion, **Δ**AIC: difference in AIC from that of the best fitting model, *w*AIC: AIC weight